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Bulletin of the British Museum (Natural History)

Geology series Vol 36 1982

British Museum (Natural History)
London 1982

Dates of publication of the parts

No 1	25 March 1982
No 2	28 October 1982
No 3	25 November 1982
No 4	23 December 1982

ISSN 0007–1471

Printed in Great Britain by Adlard & Son Ltd, Bartholomew Press, Dorking, Surrey

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British Museum (Natural History)

Middle Cambrian trilobites from the Sosink Formation, Derik–Mardin district, south-eastern Turkey

W. T. Dean

Geology series Vol 36 No 1 25 March 1982

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London SW7 5BD,
England.

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Geol.)

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The Geology Series is edited in the Museum's Department of Palaeontology.
Keeper of Palaeontology: Dr H. W. Ball
Editor of the Bulletin: Dr M. K. Howarth
Assistant Editor: Mr D. L. F. Sealy

BRITISH MUSEUM
PUBLICATIONS
ISSUED
25 MAR 1982
SALES OFFICE
NATURAL HISTORY

ISSN 0007-1471

Geology series
Vol 36 No 1 pp 1-41

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 25 March 1982

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Middle Cambrian trilobites from the Sosink Formation, Derik–Mardin district, south-eastern Turkey

W. T. Dean William Thornton
Department of Geology, University College, Cardiff CF1 1XL

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Synopsis

Trilobites from thin limestone beds in the lowest 225 m of the type section of the Sosink Formation SE of Derik include: *Peronopsis fallax* (Linnarsson 1869) aff. *minor* (Brögger 1878), *Solenopleuropsis marginata marginata* Sdzuy 1958, *Conocoryphe* (*Conocoryphe*) *caecigena* sp. nov., *Dorypyge terneki* sp. nov., *Paradoxides* (*Eccaparadoxides*) *remus* sp. nov., *P.* (*E.*) cf. *pradoanus* de Verneuil & Barrande 1860, *Paradoxides* (s.l.) *pentagonalis* sp. nov., *Chelidonocephalus anatolicus* sp. nov. and *Derikaspis toluni* gen. et sp. nov. The affinities of the fauna are largely with the western Mediterranean region, where *Derikaspis* occurs only in the Montagne Noire, SW France, but elements from Iran are also represented. A late, but not latest, Middle Cambrian age is postulated.

Introduction

The Derik–Mardin area (Fig. 1) lies between the rivers Tigris (or Dicle) and Euphrates (or Fırat) in south-eastern Turkey, about 75 km south of Diyarbakır and 25 km north of the Turkish-Syrian border. Much of the higher ground between Derik and Mardin is occupied by conspicuous outcrops of Cretaceous and Tertiary limestones, overlain by extensive Quaternary basalts which occupy the stony lower ground. Lower Palaeozoic, particularly Cambrian, rocks, transgressed by unconformable Cretaceous deposits, form a series of narrow inliers, elongated E–W, which extend some 20 km eastwards from near Derik. Knowledge of the local stratigraphy dates from 1934 when H. F. Moses produced a report on the Mardin–Cizre region for Maden Tetkik ve Arama (= M.T.A.), Ankara. Although officially unpublished, this pioneer work was quoted subsequently by Tolun & Ternek (1952) and by Tolun (1960), and a N–S cross-section (Mazı Dağ to Harabon Dağ) extracted from it was published by van der Kaaden (1971). Moses was the first to collect trilobites in the area but details of his discovery were never published, though his small collection was submitted to Professor B. F. Howell and recognized by him as being of Cambrian age. Mrs Phyllis Hasson, Princeton University, kindly allowed me to examine this material, which clearly corresponds to the fauna described in the present paper but is scanty and carries no detailed locality data. Tolun & Ternek (1952) collected further material and their paper included preliminary determinations by C. J. Stubblefield. The most important work dealing with the geology of the area is a comprehensive report by Kellogg (1960); though officially unpublished, it was nevertheless widely circulated, and thanks to the officials of M.T.A. I was able to consult the relevant portions.

Stratigraphy

The lithostratigraphic succession adopted here for the older rocks of the Derik area is as follows:

Bedinan Formation
~~~~unconformity~~~~
Sosink Formation
Koruk Formation
Sadan Formation
Derik Formation

Derik Formation. Base not seen. Comprises mostly volcanic rocks and corresponds to Derik Volcanics of Kellogg (1960), who postulated a thickness of 488+ m. Formational status, with a thickness of more than 2000 m, was accorded by Rigo de Righi & Cortesini (1964 : 1913) and by Schmidt (1965). Ketin (1966 : 77–80; pl. I) gave the same thickness but termed the unit Telbismi Formation, a name here considered best abandoned because it had been used earlier by Kellogg (1960) for reddish sandstones and shales corresponding to the present Sadan Formation.
~~~~

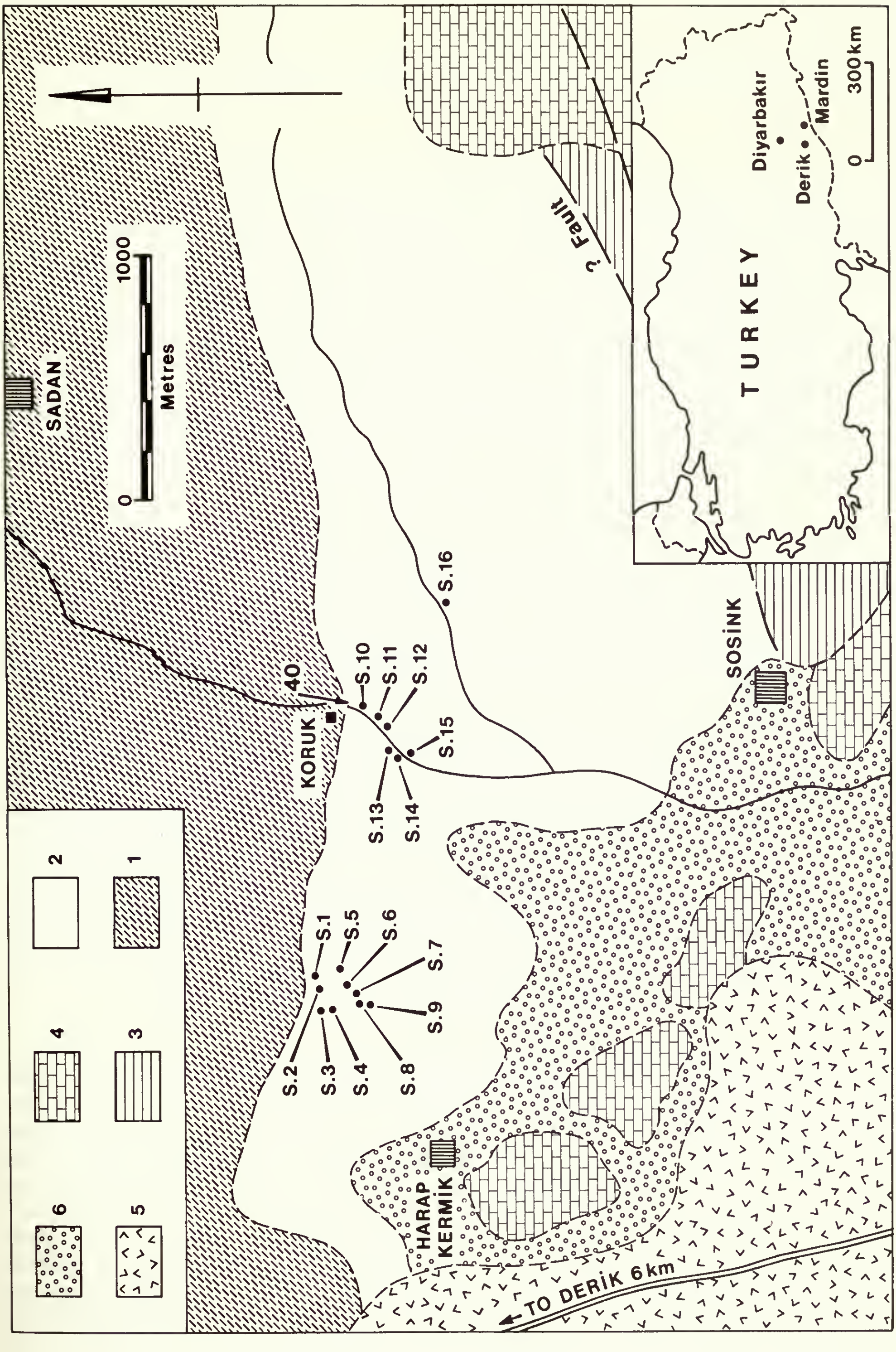

6
5
4
3
2
1
SADAN
0
1000
Metres
KORUK
40
S.1
S.2
S.3
S.4
S.5
S.6
S.7
S.8
S.9
S.10
S.11
S.12
S.13
S.14
S.15
S.16
SOSİNK
HARAP
KERMİK
TO DERİK 6 km
Fault
?
TURKEY
Diyarbakır
Derik
Mardin
0
300 km

Fig. 1 Sketch map showing fossil localities in the Sosink Formation at two sections in the area NW and north of Sosink village. Inset map shows geographical position of the area in SE Turkey. Key to lithostratigraphic units: 1, Sadan Formation and Koruk Formation (undifferentiated). 2, Sosink Formation. 3, Bedinan Formation. 4, Limestones of Cretaceous and Tertiary age (undifferentiated). 5, Quaternary basalts. 6, Recent deposits.

Sadan Formation. Introduced by Rigo de Righi & Cortesini (1964 : 1913) for 300 m (apparently an underestimate) of conglomerates, coarse sandstones and redbeds. Corresponds broadly to the now abandoned Telbesmi (originally Telbismi) Formation, 584 m thick, of Kellogg (1960). A thickness of 685 m was given by Ketin (1966 : 77–80), who used also the notation C_1, and the unit is approximately equivalent to Schmidt's (1965) combined 'Sadan Redbeds Fm' and 'Zabuk Qtzt/Ss Fm', for which no thickness was indicated.

Koruk Formation. Used first as 'Koruk Ls/Dol Fm' by Schmidt (1965) and equivalent to the Sadan Dolomite, 243 m thick, of Kellogg (1960). The unit was not differentiated by Rigo de Righi & Cortesini (1964 : 1913), who apparently included it (as '250 m intercalated lsts and dolomites') within the Sosink Formation as interpreted by them. Ketin's (1966 : 79) 'Dolomite formation (C_2)' appears to match exactly with Schmidt's (1965) 'Koruk Ls/Dol Fm' and should not be confused with Ketin's (1966 : 80) 'Sosink or Koruk formation (C_3)', which corresponds to the present usage of Sosink Formation *sensu stricto*. The Koruk Formation is named after a group of buildings, unused in summer, sited 1·8 km north of Sosink village (Fig. 1); the type section is in the banks of the immediately adjacent stream valley. During my visit in 1979 with geologists of T.P.A.O. it was agreed informally to draw the Koruk/Sosink formational boundary at the base of a sequence of shales and siltstones, and immediately above a 13·6 m limestone unit which succeeds the yellow-grey weathering dolomites that constitute the greater part of the Koruk Formation.

Sosink Formation. Introduced by Kellogg (1960) for a unit of shales which passes upwards into siltstones and sandstones, often massive and cross-bedded, in the area north and north-east of Sosink, where he measured a total thickness of 1057 m. The stream valley running south from Koruk to Sosink (Fig. 1) may be considered as type section. The unit corresponds to 'Sosink Ss/Sh Fm' of Schmidt (1965) and 'Sosink or Koruk Formation (C_3)', 1120 m thick, of Ketin (1966 : 80), but includes only the highest 1700 m (probably an overestimate) of the Sosink Formation as interpreted by Rigo de Righi & Cortesini (1964 : 1913).

The succeeding Bedinan Formation, introduced by Kellogg (1960) for an Ordovician shale sequence at Bedinan village, 15 km east of Sosink, has remained constant in usage, though its relationship to the Sosink Formation has been subject to different interpretations. It has been variously regarded as conformable (Rigo de Righi & Cortesini 1964 : 1913, Ketin 1966 : 80) or questionably conformable (Schmidt 1965). Kellogg's (1960) original assertion of a disconformity has been borne out by subsequent researches, and the fauna of the Bedinan Formation, both at Bedinan and near Sosink, indicates a mid-Caradocian age for at least part of the unit (Dean 1967). A Sosink/Bedinan formational disconformity claimed by Kellogg (1960) at Şip Dere, 7 km ENE of Sosink, has been confirmed and shown to be of considerable magnitude; the faulted relationship north-east of Sosink as shown by him, and used questionably in the present paper (Fig. 1), is less clear owing to lack of exposures.

The town of Derik is sited on the south flank of a plateau formed by Cretaceous limestones (Mardin Formation) which unconformably overlie southerly-dipping Derik Volcanics, or Derik Formation. The latter are succeeded to the south by resistant rocks of the Sadan Formation and the Koruk Formation, which often form conspicuous hills; these strata are followed in turn by more regressively-weathering shales of the lower Sosink Formation which give rise to a gently undulating topography. In the area north of Sosink village the Sosink Formation is up to 1100 m thick; the lowest third comprises silty shales and fine-grained sandstones with occasional thin bands of limestone which may sometimes be traced for tens of metres along the strike but generally die out horizontally. The limestones include some calcarenites in which glauconite may be abundant, but micrites and whitish, sparry limestones also occur. Fossils mostly comprise disarticulated and broken trilobite remains such as those described here, but some inarticulate brachiopods occur. Sometimes the trilobite fragments are so small as to preclude generic identification, but in general the material has suffered little distortion or compression and details of surface ornamentation are often preserved. Ascending the succession, the limestone horizons come to an end and the rocks become coarser, with frequent, massive beds of current-bedded sandstone. Occasional beds of silty shale are interbedded with the sandstones, and the trilobites *Holasaphus* (Dean 1972) and poorly-preserved agnostids were found in approximately the middle part of the Sosink Formation, most of which is unfossiliferous.

Acknowledgements

Collecting by Janette Dean and myself would have been impossible without the kindness, co-operation and hospitality of numerous Turkish friends and colleagues, particularly from Maden Tetkik ve Arama, Ankara. The then director, Dr Sadretin Alpan, granted us the facilities of his organization, and in Ankara Dr Cahide Kırağlı helped us obtain relevant geological literature; in the field we were ably guided by Mr Günel Aygün, as well as by Mr Abdurrahman Tunç of Derik. My subsequent visit to the area in 1979 was made possible thanks to the co-operation of geologists of T.P.A.O., Ankara. At Princeton University, Mrs Phyllis Hasson kindly made available the original collection of H. F. Moses. I am much indebted to Dr A. W. A. Rushton (I.G.S., London) for reading the manuscript and making suggestions for its improvement. Mrs Margaret Millen prepared the text-figures from my drawings, Mr Peter Green (British Museum (Natural History)) took the photographs, and Dr Mu Xi-nan translated relevant passages published in Chinese.

Systematic descriptions

The terminology employed here follows for the most part the Treatise on Invertebrate Paleontology (Harrington, Moore & Stubblefield, *in* Moore 1959 : O117). Terms for agnostids are essentially those of Palmer (1955 : 88), with minor modifications proposed by Whittington (1963 : 27). The use of 'median plectrum' is that of Öpik (1967 : 58), and the interpretation of this term, 'border furrow' and 'false border furrow' in *Chelidonocephalus* and *Derikaspis* follows Fortey & Rushton (1976 : 335–337).

All the material is from the Sosink Formation NW or north of Sosink, Turkey, and locality numbers (prefixed S.) refer to the sections shown in Figs 1 and 2, showing their geographical position and stratigraphic level respectively. Specimen numbers prefixed It. are housed in the Department of Palaeontology, British Museum (Natural History), London; material prefixed MTA is in the collection of Maden Tetkik ve Arama, Ankara.

Dimensions are given in mm; those marked * are estimated.

Class **TRILOBITA** Walch, 1771

Family **QUADRAGNOSTIDAE** Howell, 1935

Genus ***PERONOPSIS*** Hawle & Corda, 1847

Type species. By monotypy, *Battus integer* Beyrich, 1845.

Peronopsis fallax (Linnarsson, 1869) aff. ***minor*** (Brögger, 1878)

Figs 3a–d, 4, 5

1946 *Peronopsis fallax minor* (Brögger, 1878); Westergård: 38, pl. 3, figs 3–7. Includes original synonymy.

Figured material. It.2107 (Figs 3a–d), It.2108 (Fig. 4), It.2110 (Fig. 5).

Horizons and localities. All the illustrated specimens are from 80 m above the base of the Sosink Formation, at loc. S.4. On the basis of one incomplete cephalon (It.2111) the species is recorded questionably from loc. S.8, 155 m above the base of the Sosink Formation.

Other material. Ten unfigured cephala and eight pygidia, mostly fragmentary, from S.4.

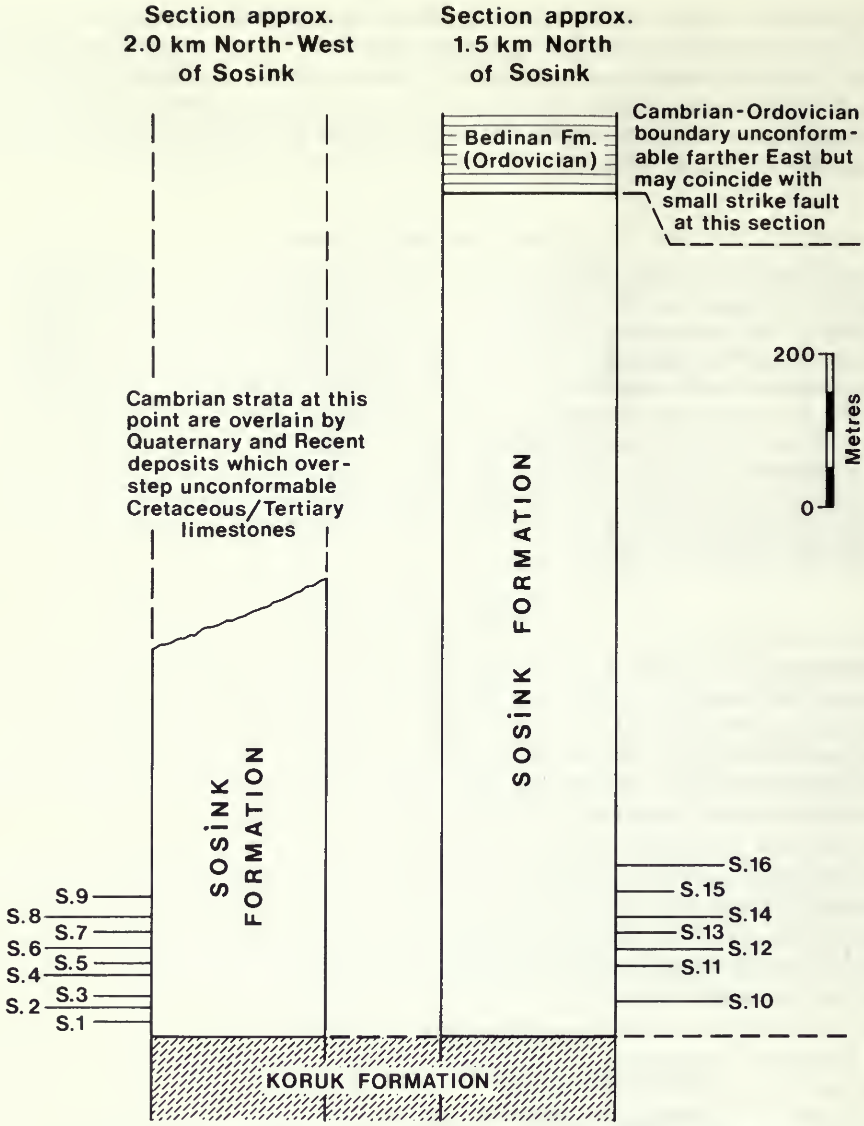
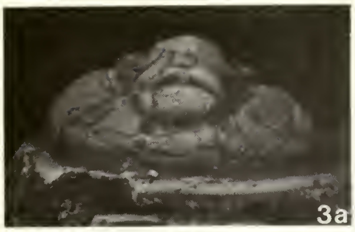

Section approx. 2.0 km North-West of Sosink
Section approx. 1.5 km North of Sosink
Bedinan Fm. (Ordovician)
Cambrian-Ordovician boundary unconformable farther East but may coincide with small strike fault at this section
200
0
Metres
Cambrian strata at this point are overlain by Quaternary and Recent deposits which overstep unconformable Cretaceous/Tertiary limestones
SOSİNK FORMATION
SOSİNK FORMATION
S.9
S.8
S.7
S.6
S.5
S.4
S.3
S.2
S.1
S.16
S.15
S.14
S.13
S.12
S.11
S.10
KORUK FORMATION

Fig. 2 Two stratigraphic sections, respectively NW and north of Sosink (see Fig. 1, p. 3), showing horizons of fossil localities in the Sosink Formation.

Figs 3–5 *Peronopsis fallax* (Linnarsson, 1869) aff. *minor* Brögger, 1878. All loc. S.4. Figs 3a–d, anterior, plan, posterior and left lateral views of almost exfoliated cephalon. It.2107, ×9. Fig. 4, internal mould of pygidium. It.2108, ×8. Fig. 5, almost complete pygidium with exoskeleton intact. It.2110, ×12.

Figs 6–10 *Solenopleuropsis marginata marginata* Sdzuy, 1958. All loc. S.1. Figs 6a, b, plan and oblique left anterolateral views of incomplete cranidium. It.1106, ×7. Fig 7, plan view of incomplete cranidium; note median occipital tubercle. It.1110. ×6. Fig. 8, part of small (meraspid?) cranidium. It. 1099. ×16. Fig. 9, almost complete cranidium showing small, smooth, left palpebral lobe. It. 1119. ×5. Fig. 10, oblique left lateral view of cranidium. Note transverse arrangement of tubercles on posterior part of glabella, and posteriorly-inclined, spine-like tubercles on occipital ring. It. 1095. ×6.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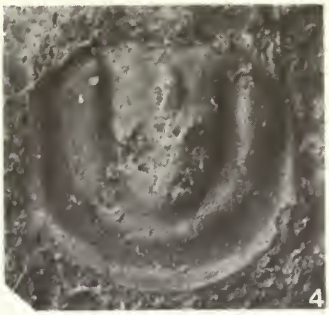
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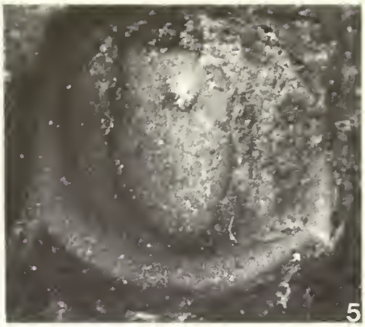
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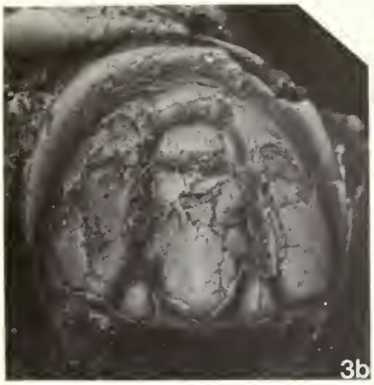
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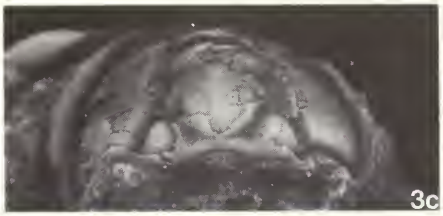
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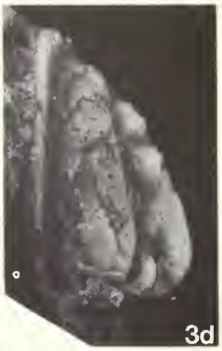
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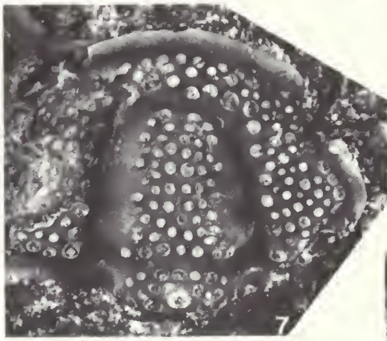
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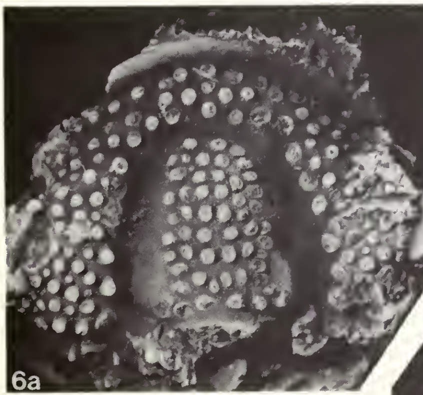
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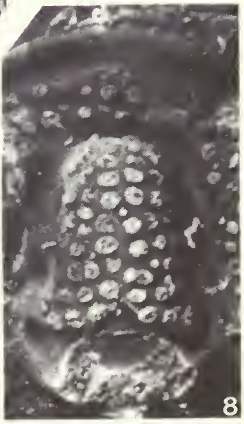
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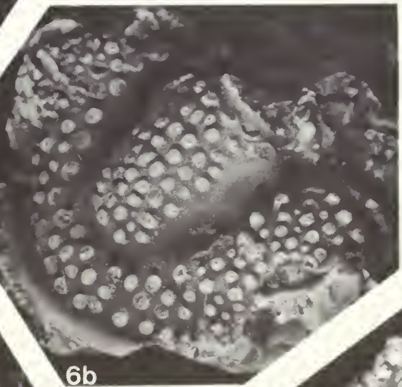
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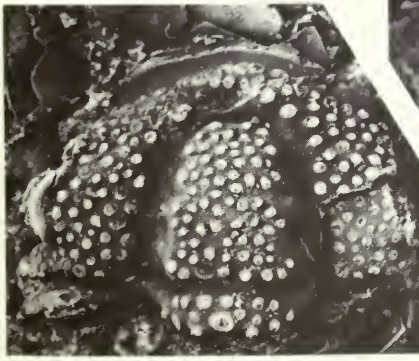
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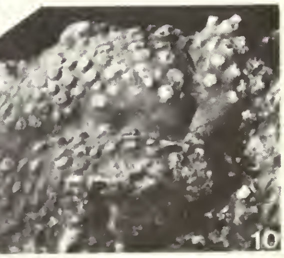
10

DIMENSIONS. Cephalon, It.2107: median length 4·5 mm, overall breadth 5·1 mm, length of axis 3·2 mm, median breadth of axis 1·5 mm. Pygidium, It.2108: overall breadth 5·2 mm*, length (excluding half-ring) 4·6 mm, length of axis 3·6 mm, frontal breadth of axis 2·9 mm*.

DESCRIPTION AND DISCUSSION. Descriptions and illustrations of *Peronopsis fallax minor* and several other subspecies of *P. fallax* were given by Westergård (1946). Further comments were made by Fortey & Rushton (1976 : 326–327) in discussing Iranian specimens determined by them as *P. fallax* aff. *minor*. Westergård's (1946: pl. 3, figs 5–7) illustrations of the pygidium of *P. fallax minor* demonstrate considerable variation in the form and relative size of the axis, and the present specimens fall within this variation; in particular It.2110 (Fig. 5) agrees closely with an original of Westergård (1946 : pl. 3, fig. 7). Fortey & Rushton (1976 : 326) noted than in *P. fallax minor* the 'pygidial flanks', a term corresponding to 'pleural lobe' of Palmer (1955 : fig. 1) and to 'pleural field' of Harrington, Moore & Stubblefield, *in* Moore (1959 : O214), are confluent behind the axis. The same feature is found in the present material, though it is less conspicuous on the external surface (Fig. 5) than on an internal mould (Fig. 4), where both border furrow and axial furrows are notably broad.

Comparison of the Turkish cephala with *P. fallax minor* is more tenuous and a largely exfoliated cephalon now illustrated (Figs 3a–d) shows two distinct pairs of lateral lobes of approximately equal length (exs.) on the posterior glabellar lobe; similar structures are clearly visible on cephala of *Peronopsis cylindrica* Westergård (1946: pl. 3, figs 17, 19, 20) and *P. quadrata* (Tullberg, 1880) (see Westergård 1946: pl. 3, figs 22, 23, 25, 26, 28) from Sweden. On the other hand the external surface of cephala from loc. S.4 shows little evidence of furrows on the posterior glabellar lobe, though the pair of glabellar lobes immediately behind the transglabellar furrow is always apparent; similar lobes, involving a slight expansion of the glabellar outline, may be seen, though less well developed, on a cranidium of *P. fallax minor* figured by Westergård (1946: pl. 3, fig. 4). The occipital lobes (Whittington 1963 : 28) are similarly more distinct on the internal mould (Fig. 3b) than on the external surface of cephala from S.4.

According to Westergård (1946 : 39) *P. fallax minor* occurs in the *Solenopleura brachymetopa* Zone, late Middle Cambrian, of Scandinavia, where its age may not be very different from that of the Sosink specimens. Closely similar material from near Nuneaton, central England, determined first as *P. fallax* cf. *minor* by Taylor & Rushton (1972 : 19; see Fortey & Rushton 1976 : 327; pl. 12, fig. 15) and later as *P. fallax minor* (Rushton 1978 : 251; pl. 24, fig. 1), came from the *Agnostus pisiformis* Zone, earliest Upper Cambrian.

Family **SOLENOPLEURIDAE** Angelin, 1854

Subfamily **SOLENOPLEUROPSINAE** Thoral, 1947

[= Saoinae Hupé, 1953].

Genus ***SOLENOPLEUROPSIS*** Thoral, 1947

TYPE SPECIES. By original designation, *Conocoryphe rouayrouxi* Munier-Chalmas & Bergeron, 1889.

Solenopleuropsis marginata marginata Sdzuy, 1958

Figs 6a, b, 7–10

1958 *Solenopleuropsis marginata marginata* Sdzuy: 245; pl. 2, fig. 7.

1961 *Solenopleuropsis marginata marginata* Sdzuy; Sdzuy: 364; pl. 27, figs 6–12; pl. 28, figs 1–7; pl. 31, fig. 7; pl. 34, fig. 6; text-fig. 46.

FIGURED MATERIAL. It.1095 (Fig. 10), It.1099 (Fig. 8), It.1106 (Figs 6a, b), It.1110 (Fig. 7), It.1119 (Fig. 9).

Horizon and locality. The species was found at only one level, 18 m above the base of the Sosink Formation, at loc. S.1, NW of Sosink.

Additional material. Fifteen cranidial fragments from loc. S.1.

Dimensions (in mm).	It.1095	It.1099	It.1106	It.1110	It.1119
Max. breadth of cranidium	–	4·5	9·5	12·0*	11·4
Median length of cranidium	7·5	3·0	6·6	7·5	7·8
Frontal breadth of cranidium	5·1	2·1	6·0*	7·0	6·5
Distance across palpebral lobes	8·8	–	8·6	10·1	10·1
Basal breadth of glabella	3·2	1·4*	3·2	3·9	4·3

Description and discussion. The present cranidia, all of which come from a single thin (5 cm) bed of limestone, exhibit some variation in glabellar proportions (possibly the result of compression) and in the number and regularity of the tubercles; they agree well with the holotype and with other specimens from Spain illustrated subsequently by Sdzuy (1961; see synonymy), some of which may have smaller, more numerous tubercles and, occasionally, four subconcentric rows in front of the glabella. Most of the other species described by Sdzuy (1958 : 242–246; 1961 : 354–373) are readily eliminated from present consideration on the basis of subangular outline of anterior border, long (sag.) preglabellar field, lack of glabellar furrows, and the large number of very small tubercles on the cranidium. *Solenopleuropsis* cf. *ribeiroi* (de Verneuil & Barrande, 1860) as figured by Sdzuy (1961 : pl. 26, figs 3–5) apparently has large tubercles like those of Turkish material on the preglabellar field but not on the glabella and posterior portions of the fixigenae, where they are much smaller. *S. ribeiroi* was considered by Sdzuy to be of doubtful validity and was rejected by Courtessole (1973 : 148). The ornamentation of large tubercles found in *Solenopleuropsis thorali* Sdzuy (1958 : 244; 1961 : 365) resembles that of the Turkish specimens but in most cases the preglabellar field has two, rather than three, concentric rows of tubercles, and their arrangement is more regular. A more reliable criterion may be the greater width (tr.) of the frontal area in *S. marginata marginata*.

Cranidia of all the several species of *Solenpleuropsis* described from the Middle Cambrian of the Montagne Noire, SW France (see Courtessole, 1973: 143–159 for review) are ornamented with smaller, more closely crowded tubercles than *S. marginata marginata* or *thorali*. In certain cases (for example, *S. rouayrouxi* (Munier-Chalmas & Bergeron, 1889), redescribed by Courtessole 1973: 148) the number of both tubercles and concentric rows of tubercles on the preglabellar field may vary widely.

Family **CONOCORYPHIDAE** Angelin, 1854

Genus ***CONOCORYPHE*** Hawle & Corda, 1847

[= *Couloumania* Thoral, 1946].

Type species. By subsequent designation of Miller, 1889, *Trilobites sulzeri* Schlotheim, 1823.

Subgenus ***CONOCORYPHE*** Hawle & Corda, 1847

Conocoryphe* (*Conocoryphe*) *caecigena sp. nov.

Figs 11a, b, 12

Diagnosis. *C.* (*Conocoryphe*) species with parabolic glabellar outline and three unequal pairs of lateral glabellar lobes; 1p and 2p glabellar furrows broad (exs.) and moderately deep, but 3p pair transverse and slit-like. Pair of protuberances, generally resembling eyes in form but lacking visual surfaces and palpebral lobes or furrows, sited opposite 3p glabellar lobes and midway between glabella and lateral border furrow. Surface of exoskeleton, excluding furrows, ornamented with closely-spaced, coarse tubercles.

HOLOTYPE. It.1121 (Figs 11a, b). Dimensions: max. breadth of cranidium 16·5 mm, median length of cranidium 8·7 mm, length of glabella and occipital ring 6·1 mm, max. breadth of glabella 5·1 mm.

OTHER MATERIAL. It.1124 (Fig. 12), and three unfigured cranidial fragments.

HORIZONS AND LOCALITIES. The holotype and the unfigured fragments are from loc. S.5, approx. 95 m above the base of the Sosink Formation at the section NW of Sosink. It.1124 is from loc. S.12, north of Sosink, at a level 115 m above the base of the Sosink Formation.

DESCRIPTION AND DISCUSSION. The new form is one of a small number of *C.* (*Conocoryphe*) species, termed 'oculé' by Courtessole (1976*b*), in which eyes are apparently represented by a pair of protuberances which lack any trace of visual surface; the animal presumably was blind. The anterior and lateral borders of the cranidium of *C.* (*C.*) *caecigena* form a continuous structure which narrows posterolaterally. The almost marginal position of the facial suture, cutting the cephalic border obliquely near the genal angles so that the librigenae must have been diminutive dorsally, matches that illustrated by Šnajdr (1958: fig. 32) for *C.* (*Conocoryphe*) *sulzeri* (Schlotheim) and by Sdzuy (1961: figs 48–53) for other members of the Conocoryphidae. There is no sign of a conventional type of facial suture linking the eye-like protuberances with the anterior and posterior borders. As for the protuberances themselves (Fig. 12), the tuberculation of the fixigenae continues onto the nearly horizontal dorsal surface but is then replaced by closely-grouped granules on the laterally-facing, almost vertical sides, which in conventional trilobites would correspond to the visual surfaces. The fixigenae become narrower frontally where they are linked by a narrow (sag.) ridge, surmounted by a single arc of tubercles, that represents the preglabellar field. The coarsely tuberculated surface of the new species, combined with the broad (exs.), smooth areas containing the very shallow lateral glabellar furrows, gives it a characteristically prickly appearance, and many of the tubercles (Fig. 11a) show a small median perforation, suggesting they are bases of broken-off spines.

Other species of *C.* (*Conocoryphe*) which bear rudimentary, eye-like protuberances generally resembling those of *C.* (*C.*) *caecigena* include the following:
C. (*C.*) *pseudooculata* Miquel, 1905, redescribed by Courtessole (1973 : 188; includes full synonymy). Middle Cambrian (Niveau F), Montagne Noire, SW France.
C. (*C.*) *palpebralis* Sdzuy (1957 : 21). Middle Cambrian, Doberlug, Germany.
C. (*C.*) *havliceki* (Šnajdr). Described originally as *Couloumania havliceki* Šnajdr (1957 : 239; 1958 : 172, 251). Middle Cambrian, *Eccaparadoxides pusillus* Zone, near Jince, Bohemia.
C. (*C.*) *ferralsensis* Courtessole (1967*a* : 501). Middle Cambrian (Niveau H), Montagne Noire, SW France.
C. (*C.*) *sdzuyi* Courtessole (1967*b* : 527). Middle Cambrian, Spain. Based on material previously attributed to *C.* (*C.*) *pseudooculata* by Sdzuy (1961 : 664).

According to Courtessole (1973 : 192), *C.* (*C.*) *pseudooculata* differs from *C.* (*C.*) *ferralsensis* in having more strongly developed protuberances (for which he used also the

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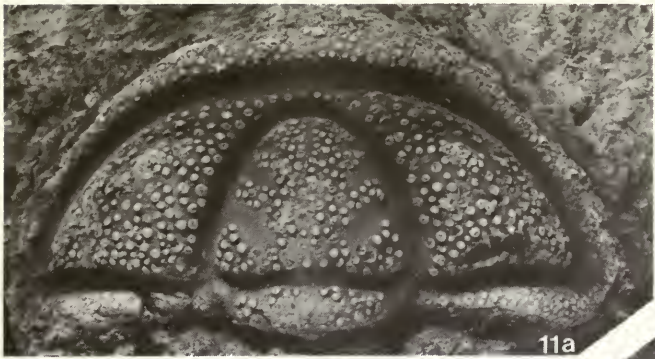
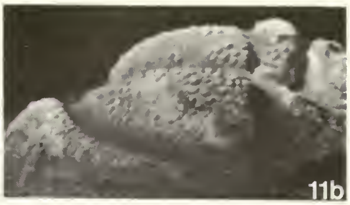
Figs 11–12 *Conocoryphe* (*Conocoryphe*) *caecigena* sp. nov. Figs 11a, b, plan and left lateral views of cranidium. **Holotype,** It.1121, × 4·5. Loc. S.5. Fig. 12, left anterolateral view of left genal region of cranidium, showing 'ocular' protuberance. Note absence of eye lenses and facial suture. It.1124, × 2·5. Loc. S.12.

Figs 13–18 *Dorypyge terneki* sp. nov. Fig. 13, hypostoma. It.2090, × 6. Loc. S.3. Figs 14a, b, anterior and plan views of pygidium showing marginal spines inclined posterolaterally. It.2076, × 4. Loc. S.4. Fig. 15, left librigena. It.1138, × 6. Loc. S.5. Fig. 16, dorsal view of partly exfoliated cranidium. **Holotype,** It.2080, × 3. Loc. S.4. Fig. 17, incomplete pygidium. MTA coll., unnumbered, × 7. Loc. S.4. Fig. 18, oblique left lateral view of incomplete cranidium with occipital spine intact. It.2077, × 4. Loc. S.4.


11a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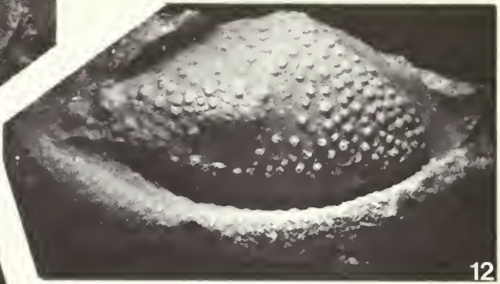
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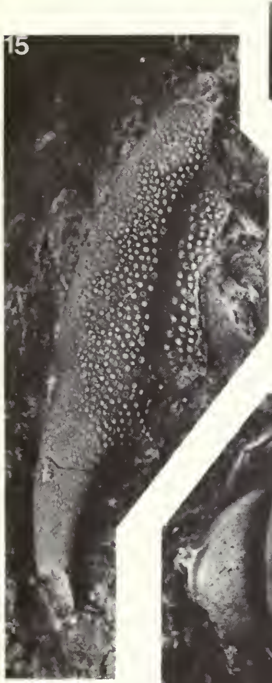
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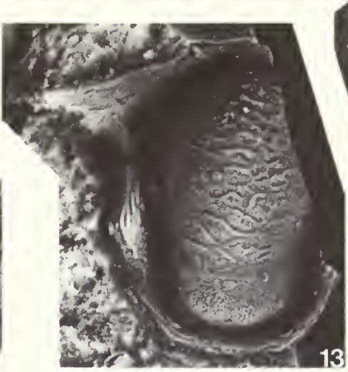
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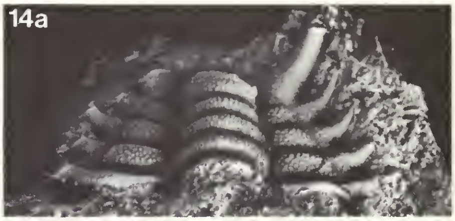
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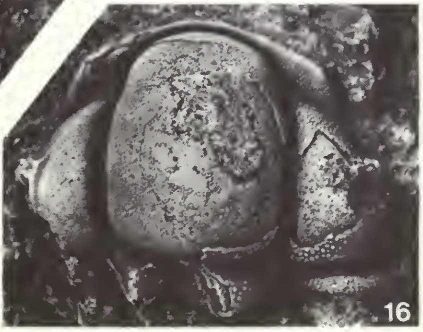
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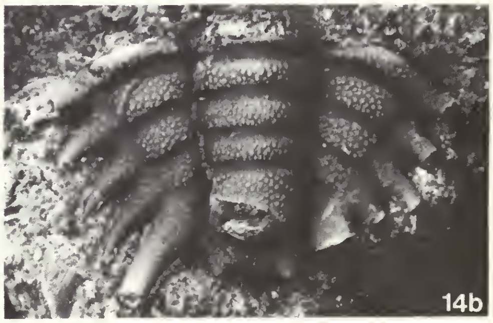
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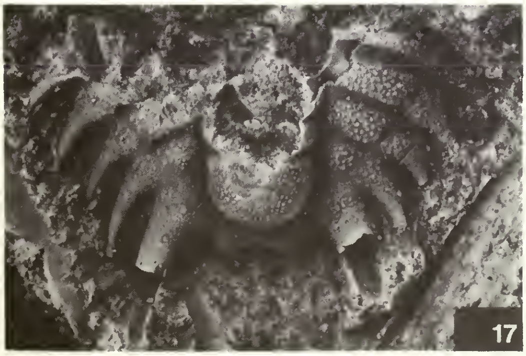
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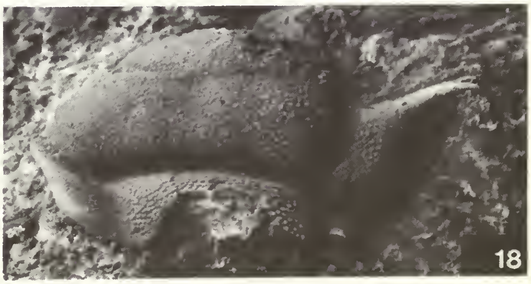

18

term 'bosse oculaire'), a shorter, subconical (compared with conico-oval) glabella and a lateral border ornamented with a single row of well-spaced tubercles, compared with two or three rows of closely-spaced tubercles. *C.* (*C.*) *caecigena* has coarser ornamentation, with fewer and conspicuously larger tubercles, than either of the two French species, but bears a closer resemblance to *C.* (*C.*) *ferralsensis* than to other described species.

C. (*C.*) *palpebralis* has a subtrapezoidal glabellar outline with poorly-differentiated glabellar lobes; the protuberances are set very close to the glabella, and the surface lacks coarse tubercles.

C. (*C.*) *havliceki* carries relatively large tubercles, though they are even sparser than in *C.* (*C.*) *caecigena*, but the glabellar outline is almost straight-sided, longer and narrower than that of the Turkish species, with poorly-defined glabellar furrows and a conspicuously long preglabellar field. *C.* (*C.*) *sdzuyi* is readily distinguished from *C.* (*C.*) *caecigena* in having ornamentation comprising smaller tubercles, protuberances which are both smaller and set closer to the glabella and a longer preglabellar field with two or three rows of tubercles.

Conocoryphe (s.l.) sp.

Figs 61–63 (p. 33)

FIGURED SPECIMENS. It.1144 (Figs 62a, b) from loc. S.1; It.1148 (Fig. 61) from loc. S.5; It.3403 (Figs 63a–c) from loc. S.13. The stratigraphic levels are respectively 18 m, 95 m and 135 m above the base of the Sosink Formation.

OTHER MATERIAL. Two fragments of pygidium from loc. S.5.

DESCRIPTION AND DISCUSSION. It.1148 and It.3403 agree essentially with the pygidium of *C.* (*Conocoryphe*) *sulzeri* (Schlotheim), from the Middle Cambrian of Bohemia, illustrated by Šnajdr (1958: pl. 33, see esp. figs 8, 9), but have a proportionately larger axis. The number of axial rings (four) and pairs of pleural furrows (four) is the same in both the Turkish and Czech material. Šnajdr's illustrations show the pleural furrows varying from well-defined to almost obsolete, and their degree of definition appears to be of little value as a distinguishing feature. A general comparison may also be made with a pygidium of *C.* (*Conocoryphe*) *brevifrons* (Thoral) from SW France illustrated by Courtessole (1973: pl. 19, fig. 7), but no useful comment can be made in the absence of the cephalon. The surface of the exoskeleton of the Sosink material is covered with closely-spaced granules and sparse, low tubercles, a form of ornamentation which suggests that the species may not be *C.* (*C.*) *caecigena*, described earlier. On the other hand Šnajdr's (1958: pl. 33, figs 1, 2, 8–10) illustrations of the pygidium of *C.* (*C.*) *sulzeri* show a smooth surface, contrasting with the tubercles ornamenting the cephalon. Similar differences in ornamentation between cephalon and pygidium in *C.* (*Conocoryphe*) are apparent in material from Spain and France illustrated by Sdzuy (1961: pl. 30, fig. 9; pl. 31, fig. 11) and Courtessole (1973: pl. 17, figs 13, 14; pl. 18, fig. 13; pl. 19, figs 7, 14–16).

It.1144 is a very small, probably meraspid, pygidium and shows only two axial rings and two pairs of pleural furrows. The surface is ornamented with closely-spaced granules and the specimen may possibly represent the same species as the pygidia described above.

Family **DORYPYGIDAE** Kobayashi, 1935

Genus ***DORYPYGE*** Dames, 1883

TYPE SPECIES. By original designation, *Dorypyge richthofeni* Dames, 1883.

Dorypyge terneki sp. nov.

Figs 13–18

DIAGNOSIS. *Dorypyge* species with two unequal pairs of poorly-defined lateral glabellar lobes. Glabellar outline constricted anteriorly to form frontal glabellar lobe which extends beyond sharply-defined border furrow to invade most of anterior border. Occipital ring carries long, backwardly-curved median spine. Pygidium (excluding spines) broader than long; one-third of its breadth occupied by straight-sided axis carrying three distinct, transversely straight axial rings and traces of a fourth. Anterior half ribs and succeeding three pairs of ribs separated by deep pleural furrows and ending in subequal pairs of curved, sharply-pointed, marginal spines; fourth ribs end in a fifth pair of spines, long, stout and recurved, between which a pair of short, pointed projections is sited on posterior margin. Surface of exoskeleton, excluding furrows, ornamented with closely-spaced small tubercles.

HOLOTYPE. It.2080 (Fig. 16).

OTHER MATERIAL. It.1138 (Fig. 15), It.2076 (Figs 14a, b), It.2077 (Fig. 18), It.2090 (Fig. 13), MTA coll. unnumbered (Fig. 17), and 53 unfigured, fragmentary specimens, comprising 20 cranidia, 9 hypostomata, 4 librigenae and 20 pygidia.

HORIZONS AND LOCALITIES. All the available specimens are from levels between 35 m and 115 m above the base of the Sosink Formation, both NW and north of Sosink. It.2090 is from loc. S.3; It.2076, It.2077, It.2080 and MTA coll. unnumbered are from loc. S.4, where the species proved most abundant; It.1138 is from S.5 and rare examples were found at S.2 and S.12.

DIMENSIONS. Cranidium, It.2080: overall median length 13 mm, maximum breadth 18·8 mm*, length of glabella and occipital ring (excluding spine) 12·6 mm, basal breadth of glabella 7·5 mm, distance across palpebral lobes 14·8 mm. Pygidium, It.2076 (excluding marginal spines): maximum breadth 8·6 mm, median length 7·9 mm, frontal breadth of axis 4·3 mm, length of axis 6·8 mm.

DESCRIPTION. Cranidium, excluding occipital spine, almost one and a half times as broad as long, strongly convex and steeply declined anteriorly. Glabella convex, standing well above adjacent portions of the fixigenae, with median breadth four-fifths the median length (excluding occipital ring). Sides of glabella distally convex, curved; outline parallel-sided posteriorly but narrowing anteriorly to the broadly rounded frontal glabellar lobe, whose breadth is just more than three-quarters that of the glabella. Frontal glabellar lobe is subangular in plan, and immediately behind is a pair of ill-defined indentations which coincide with the narrower outline noted above (Fig. 16). Unequal 1p and 2p lateral glabellar lobes together occupy more than half the length of the glabella; 1p and 2p furrows are scarcely visible and there is a mere trace of a 3p pair. Large occipital ring is produced to form a sharp occipital spine that curves upwards and back. Palpebral lobes are set high on the fixigenae, opposite approximately the hindmost third of the glabella; weak eye ridges die out without reaching the axial furrows. Anterior branches of the facial suture are subparallel as far as the anterior border and then turn adaxially to cut the margin at an obtuse angle; posterior branches curve evenly to the posterior border, which turns forwards abaxially beyond the fulcra. Anterior border is broadest (exs.) and flat abaxially, and set almost at right angles to the convex fixigenae, from which it is separated by a distinct border furrow; adaxially the border diminishes to a narrow rim circumscribing the front of the glabella. A single librigena (Fig. 15) shows the border widening markedly near the genal angle, which is produced to form a stout, incurved, librigenal spine.

The hypostoma (Fig. 13) is typical for the genus, with middle body divided into two lobes, the posterior lobe occupying one-fifth the median length. The more convex anterior lobe carries ornamentation comprising anastomosing ridges and is separated from the low, granulated posterior lobe by a faint middle furrow with a pair of weakly developed maculae. The rim-like border extends laterally to form a pair of subtriangular anterior wings.

The well-segmented pygidium is strongly convex, with axis that stands high above the pleural regions and occupies two-fifths of the breadth and almost all the median length. Straight sides of the axis converge gently to the bluntly rounded tip, and three-fifths of its length (excluding articulating half-ring) are occupied by three large, subequal, axial rings; the latter are delimited by transversely straight, deep, ring furrows and there is a faint fourth ring furrow. Pleural regions carry five pairs of deep pleural furrows, and the ribs, together with the pair of anterior half-ribs, are produced posterolaterally to form stout, sharply-pointed, backwardly curved marginal spines. Anterolateral margin of the anterior half ribs forms a pair of small, steeply declined facets. First four pairs of marginal spines are almost equisized, followed by a large fifth pair, between which the margin of the postaxial field carries a pair of small, short projections just inside the line of the axial furrows. In anterior view (Fig. 14a) the marginal spines, from first to fifth, are seen to turn progressively more strongly abaxially upwards, apparently corresponding to the resting position of the animal on the sea-floor; one large, possibly gerontic, unfigured pygidium (It.1139) has the fifth pair of spines recurved adaxially.

DISCUSSION. Schrank's (1977 : 145) redescription of *Dorypyge richthofeni* Dames, 1883 from the Middle Cambrian of Wulopu, China, shows that *D. terneki* differs in minor respects, though the two are certainly congeneric. In *D. richthofeni* the posterior three-quarters of the glabella expands forwards, compared with the subparallel outline in *D. terneki*; the anterior border is less inclined frontally and the border furrow is much less distinct. The occipital spine is of similar form and size in both species. The pygidium of *D. richthofeni* is proportionately longer and its larger axis has a longer terminal piece; the first four pairs of marginal spines are straighter, directed posterolaterally instead of curving backwards. The posterior margin between the large fifth spines is blunt in some examples of *D. richthofeni*, but two specimens (Schrank 1977: pl. 2, fig 4) have a pair of distinct, slim spines; none shows short, pointed projections like those of *D. terneki*. Tubercles ornamenting the cranidium of *D. richthofeni* are much coarser than in the Turkish species, but those on the pygidium are similar. Schrank (1977 : 143) proposed a scheme showing changes in the number and disposition of marginal spines on the pygidium of *Dorypyge* throughout the Middle Cambrian; on the basis of this feature, *D. terneki* would be intermediate between *D. aenigma* (Linnarsson, 1869) and *D. richthofeni*, at a level approximating to the highest part of the *Paradoxides paradoxissimus* Stage. The irregular distribution of spines along the margin of *D. aenigma* as shown diagrammatically by Schrank does not correspond with the evenly-spaced spines illustrated by Westergård (1948: pl. 2, figs 8a, b) for the species.

The hypostoma of *D. terneki* (Fig. 13) is proportionately longer, with outline less arched frontally, than that of *D. richthofeni* (see Schrank 1977: pl. 2, fig. 5), and has more pointed anterior wings. In all these features, plus the ornamentation of anastomosing ridges, there is a remarkably strong resemblance to the hypostoma of *Dorypyge aenigma* (Linnarsson, 1869), from the *Solenopleura brachymetopa* Zone, late Middle Cambrian, of Västergötland, Sweden, redescribed by Westergård (1948 : 7; pl. 2, figs 1–8). Pygidia of the two species are closely similar, including the number and form of the axial rings. Differences are minor, but the marginal spines of *D. aenigma* are slimmer and straighter and there is no evidence of a sixth pair immediately behind the axis; Westergård (1948 : 9) considered the large, fifth pair to be the last. The glabella of *D. aenigma* is broader anteriorly than that of *D. terneki*, the constriction of the frontal glabellar lobe is less in evidence, the anterior branches of the facial suture are less convergent anteriorly and the librigenal spines are slimmer. Both species carry similar ornamentation of closely-spaced, small tubercles.

Of the Middle Cambrian species and subspecies of *Dorypyge* from Iran described by Kushan (1973), *D. iranensis iranensis* Kushan (1973 : 136; pl. 26, figs 1–6; text-fig. 9) and *D. iranensis reticulata* Kushan (1973 : 136; pl. 26, figs 7–10) appear most relevant to the present discussion. Both have a glabellar outline that is narrower at the occipital ring and expands forwards, and the anterior margin of the cranidium is more broadly rounded than in the Turkish species. The pygidium of both subspecies carries six pairs of marginal spines, but that of *D. iranensis iranensis* has four well-defined axial rings and smaller, slimmer, first to fourth marginal spines than *D. terneki,* though the sixth spines are slightly longer. The pygidium of *D. iranensis reticulata* is proportionately longer than either of the above, with only three axial rings, a notably longer terminal piece, and shorter first to fourth marginal spines.

Comparison of *Dorypyge terneki* with deformed examples of *D. asturiana* Sdzuy (1958: 240; pl. 1, figs 6, 7; 1961 : 335; pl. 22, figs 8–16, text-fig. 31), from the middle of the *Solenopleuropsis* horizon in northern Spain, is difficult. Sdzuy's illustrations suggest a glabella which expands anteriorly and lacks a constricted frontal lobe; the pygidium is wider frontally, lacks any trace of sixth marginal spines, and has only three axial rings.

Although Courtessole's (1973) revision of the Middle Cambrian trilobites of the Montagne Noire, SW France, did not list *Dorypyge*, the genus was reported previously from the area, though not described. Thoral (1935 : 61, 70, 76) noted an earlier record by Miquel at Coulouma and listed the genus from the 'Zone à *Conocoryphe Levyi*', said to be in the upper half of the middle Acadian (Acadian = Middle Cambrian).

Family **PARADOXIDIDAE** Hawle & Corda, 1847

Subfamily **PARADOXIDINAE** Hawle & Corda, 1847

Genus ***PARADOXIDES*** Brongniart, 1822

Type species. By subsequent designation of Barrande, 1852, *Entomostracites paradoxissimus* Wahlenberg, 1821.

Subgenus ***ECCAPARADOXIDES*** Šnajdr, 1957

Type species. By original designation, *Paradoxides pusillus* Barrande, 1846.

The classification of *Paradoxides* and allied trilobites is confused and in need of revision. Westergård (1953 : 34; pl. 8, fig. 2) noted and illustrated the type specimen of *P. paradoxissimus* but did not undertake a review of the genus. Šnajdr (1957, 1958) maintained the generic status of *Hydrocephalus* Barrande, 1846 and introduced the three new genera *Eccaparadoxides*, *Acadoparadoxides* and *Luhops*, all founded on type species from the Middle Cambrian of Bohemia, which received only brief mention in the Treatise on Invertebrate Paleontology (Poulsen *in* Moore 1959 : O213). *Hydrocephalus* was listed by Poulsen as a junior subjective synonym of *Paradoxides*. Sdzuy's (1961: 317–334) account of Middle Cambrian trilobites from northern Spain recognized only *Paradoxides*, but Courtessole (1973 : 123) preferred to regard *Acadoparadoxides* and *Eccaparadoxides* as subgenera of *Paradoxides* in describing Middle Cambrian faunas from the Montagne Noire, SW France. Dr A. W. A. Rushton (personal communication, 1980) has drawn my attention to the fact that *Phanoptes pulcher* Hawle & Corda (1847 : 17; pl. 2, fig. 2), the type species by monotypy of *Phanoptes* Hawle & Corda (1847 : 16), was placed by Šnajdr (1958 : 116; pl. 20, fig. 7) in subjective synonymy with *Eccaparadoxides pusillus*. By implication *Phanoptes* should therefore have priority over *Eccaparadoxides*. *Phanoptes pulcher* was founded on a meraspid, said in the original description to be 1 mm long, from Skryje, Bohemia, and *Phanoptes* has not passed into general use, being placed in synonymy with *Paradoxides* by Poulsen (*in* Moore 1959: O213). Šnajdr did not press the point and I propose to follow him in using *Eccaparadoxides*, though as a subgenus of *Paradoxides*, to accommodate most of the Sosink Formation's paradoxidids. The Turkish material adds little to our knowledge of *Acadoparadoxides*; pygidia from the higher part of the fossiliferous section at Sosink have some features in common with that of the type species, but differ in other respects and so are assigned to *Paradoxides* (s.l.).

Paradoxides* (*Eccaparadoxides*) *remus sp. nov.

Figs 19–24, 27–32

Diagnosis. Characteristics of cephalon typical for subgenus but surface of glabella in small cranidia is granulate; that of large specimens carries low tubercles, especially on frontal lobe.

Surface of fixigenae and of pygidium lacks ornamentation. Pygidium typically three-fifths as broad as long, with greatest breadth just behind centre, where confluent anterior and lateral margins form continuous curve or very slight angulation in outline. Low axis, *c*. two-fifths overall length, is subtriangular in outline; poorly defined tip grades into faint postaxial ridge that traverses most of otherwise dorsally concave surface of confluent unfurrowed pleural regions. Axis shows faint traces of two axial rings. Tip of pygidium forms pair of short points, separated by narrow (tr.), curved notch.

Holotype. It.2166 (Fig. 32).

Other material. It.1089 (Fig. 22), It.1092 (Fig. 21), It.1093 (Fig. 19), It.2201 (Fig. 20), It.2161 (Fig. 23), It.2169 (Fig. 31), It.2218 (Fig. 24), It.2226 (Fig. 28), It.2229 (Fig. 29), It.2238 (Fig. 27) and It.2239 (Figs 30a, b). Also 74 other unfigured, mostly fragmentary specimens, distributed as follows: 16 (two of them pygidia) from S.3, 9 (two pygidia) from S.4, 3 (two pygidia) from S.5, 18 (three pygidia) from S.11, 16 (three pygidia) from S.12 and 12 (one pygidium) from S.13.

Localities and horizons. Locs S.3, S.4, S.5, S.11, S.12 and S.13; these range from 53 m to 135 m above the base of the Sosink Formation. *P.* (*E.*) cf. *remus* (see p. 19) was found at S.2, 35 m above the base of the formation.

Dimensions (in mm). Cranidia	It.1092	It.2218	It.2226	It.2229	It.2239
Median length of cranidium	20·6	6·6	2·5	3·4	20·5*
Median length of glabella and occipital ring	19·2	5·8	2·2	2·9*	18·9
Max. breadth of glabella	12·6	3·6	1·2	1·8	12·7
Breadth (tr.) of occipital ring	9·4	2·9	1·0*	1·2*	9·5
Max. breadth (tr.) of frontal area	–	7·3*	2·9	3·9*	–
Distance across palpebral lobes	22·2	7·5*	2·9	3·9*	21·6*

Dimensions of holotype pygidium: median length, excluding articulating half-ring and marginal spines, 7·8 mm, maximum breadth 5·9 mm, median length of axis 3·6 mm, frontal breadth of axis 3·9 mm.

Description and discussion. Šnajdr's (1957 : 238; 1958 : 114, 248) accounts of the characteristic features of *Eccaparadoxides* may be summarized (with appropriate modifications of terminology) as follows: glabellar outline pear-shaped, with four pairs of lateral furrows, the 1p and 2p pairs transglabellar; no preglabellar field present on large cranidia, though well developed on meraspids; palpebral lobes abaxially convex in plan, very long, and extending from near axial furrows almost to posterior border furrow; posterior branches of facial suture very short; pygidial outline elongate, subhexagonal, with short (less than half overall length of pygidium), triangular axis, wide doublure, and a posterior margin which may be concave or carry one or two pairs of marginal spines.

The new species clearly fulfils the requirements of *P.* (*Eccaparadoxides*) and shares all the above features with the type species *P.* (*E.*) *pusillus* Barrande, 1846 from Skryje, Bohemia, redescribed by Šnajdr (1957 : 238; 1958: 116, 248). Large cranidia figured by Šnajdr are slightly deformed but have deeper palpebral furrows and 3p and 4p glabellar furrows; the anterior branches of the facial suture are less divergent forwards, and the lateral extensions of the frontal area are shorter (tr.) (compare Fig. 27 with Šnajdr 1958 : pl. 21, figs 6, 11). Similar criteria apply to small cranidia of both species, in which the preglabellar field is relatively long (sag.), with the additional difference that the 2p transglabellar furrow is conspicuously deeper in *P.* (*E.*) *pusillus*.

During ontogeny of *P.* (*E.*) *remus* the mesial longitudinal ridge in front of the glabella disappeared, the preglabellar field became progressively reduced so that glabella and anterior border were eventually separated by a single furrow, palpebral furrows became weaker and are virtually absent from largest examples, and the 3p and 4p glabellar furrows deepened while the 2p transglabellar furrow became both shallower and more sinuous medially. Small cranidia (Figs 22, 24) show the surface of the glabella (but not fixigenae) granulate; large examples have numerous low tubercles, particularly on the frontal lobe where some tubercles show traces of a median perforation. In his account of *P.* (*E.*) *granulosus* from SW France, Courtessole (1973 : 131; pl. 8, figs 4, 5) emphasized the importance of the granulose surface, which he had observed elsewhere only in *Paradoxides forchhammeri* Angelin, 1854, a species with small eyes and short pygidium assigned by Bergström & Levi-Setti (1978) to *Paradoxides* sensu stricto. On the other hand Lake (1935: 205) showed that tuberculation is present, though not always preserved, on the exoskeleton of *Paradoxides davidis* Salter, 1863, from the Middle Cambrian of south Wales; the feature may be more common than has been appreciated.

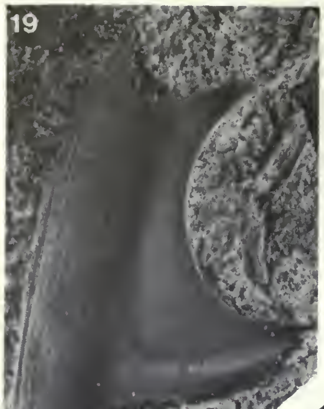
Librigenae (Fig. 19) are typical for the genus but emphasize the diminutive posterior branch of the facial suture and the transverse direction of the anterior branch on to the border, where it curves sharply forwards through a right-angle to cut the margin.

The hypostoma of *P.* (*Eccaparadoxides*) is a relatively conservative structure and apparently of limited use in differentiating species. It.2201 (Fig. 20) is closely similar to the hypostoma of *P.* (*E.*) *pusillus* illustrated by Šnajdr (1958 : pl. 21, figs 8, 9, 17, 18); minor differences include the longer posterior lobe and spines, and the longer, almost parallel-sided posterior portions of the lateral border in *P.* (*E.*) *remus.*

Essentially similar hypostomata from France were figured by Courtessole (1973: pl. 7, fig. 4; pl. 9, fig. 8) for *P.* (*E.*) *brachyrachis* Linnarsson, 1883 and *P.* (*E.*) *macrocercus* Courtessole, 1967 but detailed comparison of such deformed material is difficult. Hypostomata of *P.* (*E.*) *pradoanus* de Verneuil & Barrande, 1860 (Sdzuy 1961 : pl. 20, figs 10–14) from northern Spain similarly are not readily distinguished from those of the French species or that of *P.* (*E.*) *remus*; apparent differences include the proportionately longer lateral border and longer posterior spines of the Turkish species, criteria difficult to assess when mechanically deformed.

Fragmentary thoracic segments (Fig. 31) are typical for the genus and may carry, in addition to the usual subparallel terrace lines, tubercles similar to those on the glabella.

In discussing pygidia of *P.* (*Eccaparadoxides*) from the Montagne Noire, SW France, Courtessole (1973 : 123) observed that Šnajdr's criterion of a generally hexagonal outline applied only to *P.* (*E.*) *rouvillei* Miquel, 1905 and *P.* (*E.*) *mediterraneus* Pompeckj, 1901; on the other hand he considered pygidia of *P.* (*E.*) *brachyrachis* Linnarsson, 1883, *P.* (*E.*) *melaguensis* Thoral, 1935 and *P.* (*E.*) *macrocercus* (Courtessole, 1967) to have a different, non-hexagonal outline, expanded laterally, constricted posteriorly and ending in a pair of strong spines. Alternatively one may regard all the above, together with *P.* (*E.*) *pusillus* Barrande, 1846 and *P.* (*E.*) *pradoanus* de Verneuil & Barrande, 1860 (see p. 19) as having pygidia of a basically hexagonal, often elongated outline, the postaxial portion of which occupies from about 45% to more than 80% of the median length; the long spines of *P.* (*E.*) *brachyrachis* and *P.* (*E.*) *macrocercus* do not change this basic concept. The paddle-like pygidium of *P.* (*E.*) *remus*, with its median length 1·5–1·7 times the maximum breadth, appears to belong to the same group of species. The pygidium of *P.* (*E.*) *pusillus*, redescribed by Šnajdr (1958 : 116), has a much narrower axis than that of *P.* (*E.*) *remus*; the pleural regions are wider and the paired terminal spines are set farther apart, though the median notch separating them is shallow and broadly rounded. Following Courtessole's (1973 : 122 *et seqq.*) revision, *P.* (*E.*) *remus* differs from other species as follows: the pygidial outline is narrower, the axis longer, and the terminal piece shorter than in either *brachyrachis* or *melaguensis*; the postaxial length is conspicuously less than in *macrocercus*, in which species the outline narrows and then expands to the longer terminal spines; the postaxial length is greater than in *mediterraneus* or *rouvillei*, both of which have the posterior margin either transversely truncate or slightly convex.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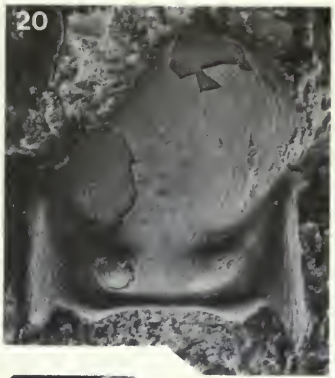
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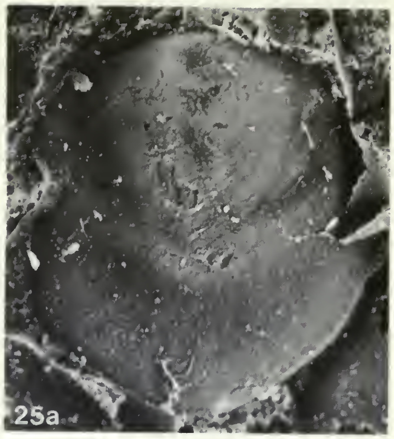
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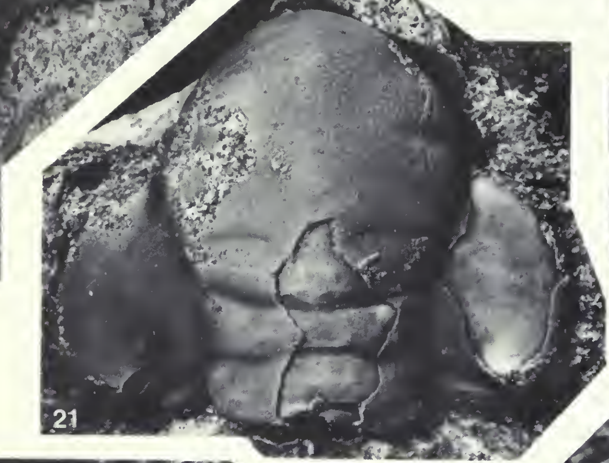
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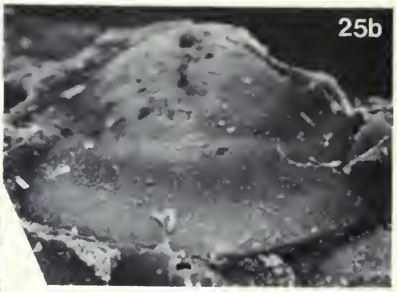
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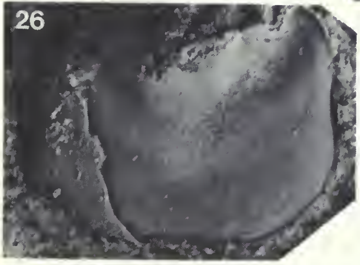
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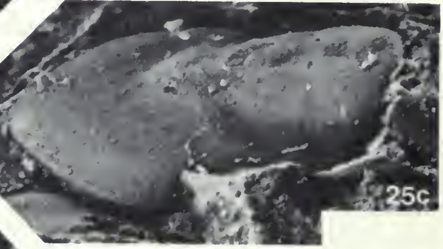
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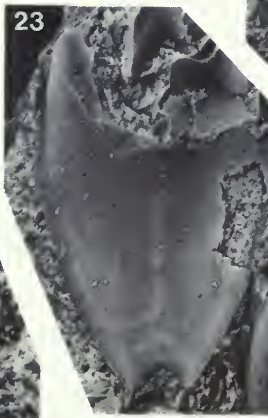
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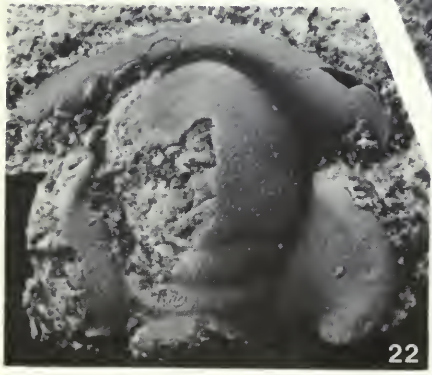
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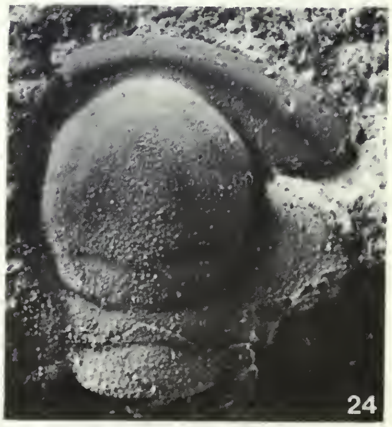
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***Paradoxides* (*Eccaparadoxides*) cf. *remus* Dean, herein**
Figs 33–35

FIGURED MATERIAL. It.2153 (Fig. 35), It.2154 (Fig. 34), It.2190 (Fig. 33).

HORIZON AND LOCALITY. 35 m above the base of the Sosink Formation, at loc. S.2.

DIMENSIONS. Pygidium, It.2154: median length, excluding articulating half-ring and marginal spines, 9·6 mm, maximum breadth 7·1 mm, median length of axis 4·0 mm, frontal breadth of axis 4·2 mm*.

DESCRIPTION AND DISCUSSION. It.2154 (Fig. 34), with bifid posterior margin, generally resembles the pygidium of *P.* (*E.*) *remus* but is proportionately broader, with shorter axis. The specimen occurs stratigraphically below the first undoubted *P.* (*E.*) *remus* and bears a stronger resemblance to that species than to the still older *P.* (*E.*) cf. *pradoanus* (below). An associated left librigena (Fig. 33) is indistinguishable from that of *P.* (*E.*) *remus*, and an incomplete pygidium (Fig. 35) is unusual in that the tip forms a single, blunt point.

The pygidium of the trilobite described by Cobbold (1911 : 286; pl. 24, figs 14–16) as '*Paradoxides rugulosus* Corda' (a species put in the synonymy of *Eccaparadoxides pusillus* by Šnajdr, 1958 : 116) from the Middle Cambrian of Comley, Shropshire, has a bifid tip like that of *P.* (*E.*) *remus* but is proportionately wider, with a longer axis and well-developed, convex pleural fields.

***Paradoxides* (*Eccaparadoxides*) cf. *pradoanus* de Verneuil & Barrande, 1860**
Fig. 36

cf. 1860 *Paradoxides pradoanus* de Verneuil & Barrande: 526; pl. 6, figs 4–6 only (*fide* Sdzuy, 1961: 322).

cf. 1961 *Paradoxides pradoanus* de Verneuil & Barrande; Sdzuy: 322; pl. 17, figs 15, 16; pl. 18, figs 1–28; pl. 19, figs 1–18; pl. 21, fig. 13; pl. 28, fig. 15; pl. 29, fig. 2; pl. 34, fig. 1; text-fig. 26. Includes synonymy.

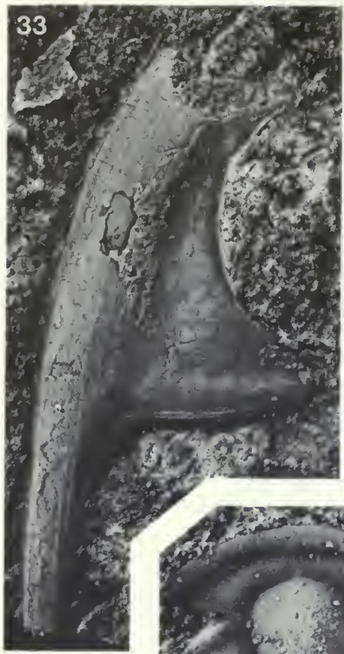
FIGURED SPECIMEN. It.1077, from loc. S.1, 18 m above the base of the Sosink Formation.

OTHER MATERIAL. Unfigured pygidium It.1075, from S.1. Ten fragments of cranidia, librigenae and thoracic segments, also from S.1, may belong here but are insufficient for specific determination.

DESCRIPTION AND DISCUSSION. The two available pygidia agree well with Sdzuy's illustrations of the species, based on material from northern Spain. The axis, excluding articulating half-ring, is triangular in outline with one weakly developed axial ring, and that of It.1007 shows traces of low tubercles. The length of the axis is no more than 27% and 29% of the overall length in It.1075 and It.1077 respectively, and may have been less as both

Figs 19–24 *Paradoxides* (*Eccaparadoxides*) *remus* sp. nov. Fig. 19, latex cast of left librigena with well-developed terrace lines along margin. It.1093, ×2·5. Loc. S.12. Fig. 20, almost complete hypostoma. It.2201, ×3. Loc. S.4. Fig. 21, large cranidium with well-developed granular ornamentation on anterior half of glabella. It.1092, ×3. Loc. S.12. Fig. 22, incomplete small cranidium with granulate glabellar surface. It.1089, ×4·5. Loc. S.12. Fig. 23, incomplete pygidium with bifid termination and faint postaxial ridge. It.2161, ×5. Loc. S.4. Fig. 24, small cranidium with granules particularly well developed on surface of occipital ring and 1p and 2p glabellar lobes. It.2218, ×7. Loc. S.4. See also Figs 27–32.

Figs 25–26 *Paradoxides* (s.l.) *pentagonalis* sp. nov. Loc. S.7. Figs 25 a–c, dorsal, posterior, and oblique right lateral views of latex cast of pygidium. Note three shallow depressions, along axial line, which represent position of articulating and ring furrows. **Holotype**, It.2158, ×8. Fig. 26, incomplete exfoliated pygidium, questionably referred to the species, in which both posterior and lateral margins are almost straight. The low ridge bounding the axis resembles that seen on the holotype. It.2159. ×6.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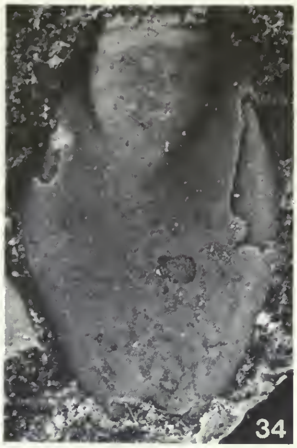
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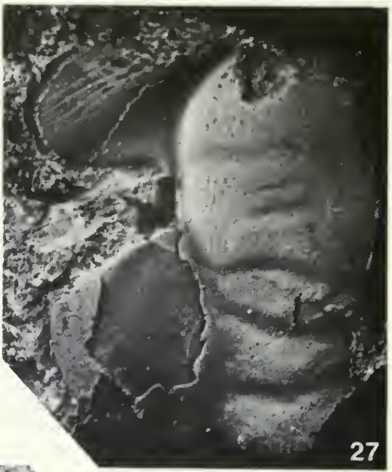
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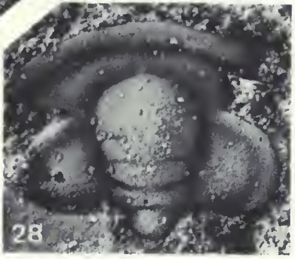
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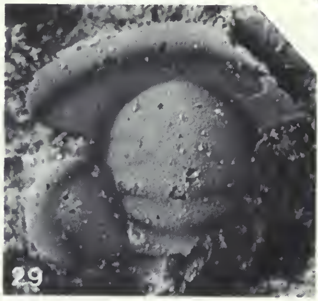
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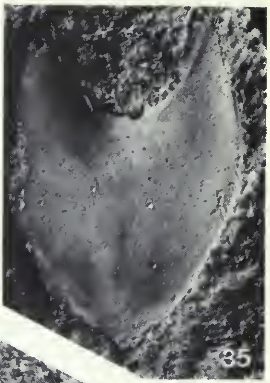
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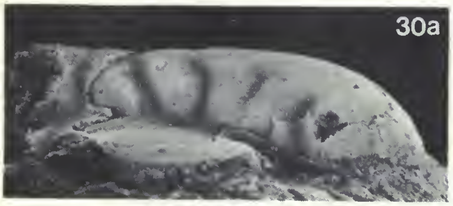
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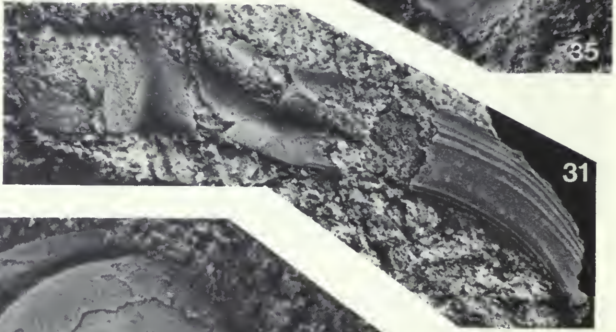
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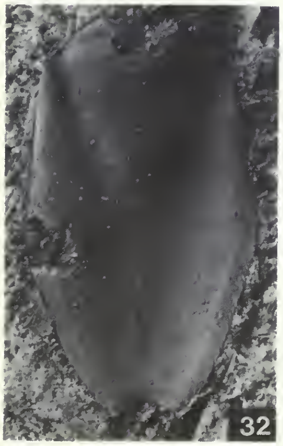
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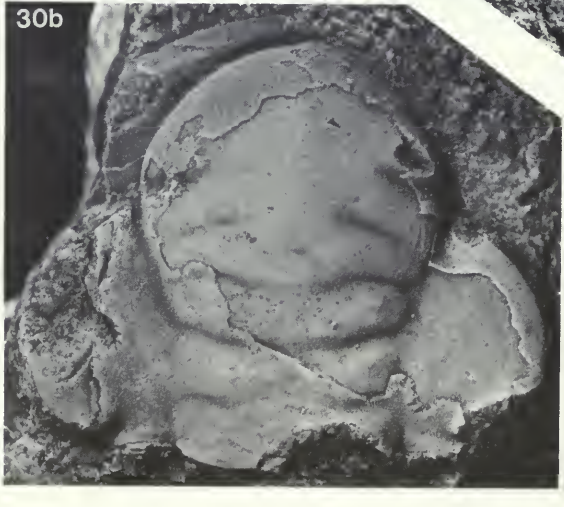
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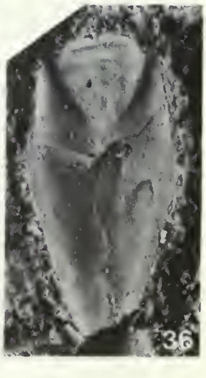
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pygidia have the tip broken off. The axis is not only considerably shorter and more strongly tapered than that of *P.* (*E.*) *remus*, but also proportionately narrower frontally (equal to about 50% of the maximum pygidial breadth compared with 70%). Broad, shallow axial furrows become obsolete near the tip of the axis, the terminal piece of which merges with the conjoined pleural regions. Axis extends about halfway to the point of maximum breadth of the pygidium, which marks the posterior limit of a pair of weakly-developed, downturned flanges that represent facets. Behind the point of maximum breadth the pygidial outline narrows only a little less markedly than in *P.* (*E.*) *pradoanus* as figured by Sdzuy (1958 : pl. 19, figs 14–18).

Paradoxides (s.l.) ***pentagonalis*** sp. nov.

Figs 25a–c, ? 26

DIAGNOSIS. Pygidium approximately as broad as long, with subpentagonal outline; subparallel sides represent facets. Pygidial tip usually bluntly pointed but may be subrounded. Axis subtriangular, circumscribed by shallow axial furrows which deepen anterolaterally; pleural fields represented by low, continuous ridge which is widest (sag.) medially and merges with terminal piece of axis, but diminishes anterolaterally. Border wide, gently declined. Position of articulating furrow and one or two ring furrows suggested by very shallow, median depressions. Surface finely granulate when viewed under high magnification.

HOLOTYPE. It.2158 (Figs 25a–c).

OTHER MATERIAL. It.2163, It.2165, and incomplete cranidia It.2157 and It.2162. It.2159 (Fig. 26) is referred questionably to the species.

LOCALITY AND HORIZON. All the specimens are from a weathered 5 cm bed of glauconitic calcarenite at loc. S.7, NW of Sosink; the stratigraphic level is 135 m above the base of the Sosink Formation.

DIMENSIONS (in mm).	It.2148	It.2158	It.2163	It.2165
Median length of pygidium (excluding half-ring)	5·3	6·4	6·3*	6·5
Maximum breadth	5·1	6·4	6·9	6·1
Length of axis	2·8	3·2	2·9	3·2
Frontal breadth of axis	3·4	4·0	4·6	4·0

Figs 27–32 *Paradoxides* (*Eccaparadoxides*) *remus* sp. nov. Fig. 27, fragmentary left half of cranidium showing anterior branch of facial suture and four pairs of lateral glabellar furrows. It.2238, × 3·5. Loc. S.3. Fig. 28, latex cast of meraspid cranidium with preglabellar field and median ridge. It.2226, × 12. Loc. S.3. Fig. 29, incomplete small (meraspid ?) cranidium. It.2229, × 10. Loc. S.11. Figs 30a, b, right lateral and dorsal views of incomplete large cranidium. It.2239, × 3. Loc. S.3. Fig. 31, part of thoracic segment, with ornamentation comprising tubercles and terrace lines. It.2169, × 3·5. Loc. S.3. Fig. 32, pygidium showing concave dorsal surface of confluent pleural regions, faint postaxial ridge and notched posterior margin with pair of terminal points. **Holotype,** It.2166, × 5. Loc. S.11. See also Figs 19–24.

Figs 33–35 *Paradoxides* (*Eccaparadoxides*) cf. *remus* Dean, herein. Loc. S.2. Fig. 33. left librigena. It.2190, × 2·5. Fig. 34, latex cast of pygidium. It.2154, × 5. Fig. 35, incomplete pygidium with single terminal point in place of the more usual two. It.2153, × 4.

Fig. 36 *Paradoxides* (*Eccaparadoxides*) cf. *pradoanus* de Verneuil & Barrande, 1860. Loc. S.1. Incomplete pygidium with very small axis; line of maximum breadth set relatively far forwards. It.1077, × 4.

DESCRIPTION AND DISCUSSION. The species is known with confidence only from the pygidium, though undetermined fragments of a cranidium, hypostoma, librigena and thoracic segments of *Paradoxides* (s.l.) were found at the type locality. The weak development of median depressions is unusual, and more clearly visible on the internal mould than on the external surface. The apparent lateral margins of the pentagonal outline correspond to the articulating facets; the low ridge, weakest anterolaterally and broadest (sag.) behind the axis, represents the pleural fields and marks the inner margin of the doublure (seen on unfigured paratype It.2163). A generally similar ridge is visible on pygidia of *Acadoparadoxides sacheri* (Barrande, 1852), type species of the genus, illustrated by Šnajdr (1958 : pl. 16, figs 6, 8–14, 16, 17) but the facets of the Bohemian species are more divergent posteriorly, the first ring furrow is deeper, and the combined axis and pleural fields are proportionately longer. Similar criteria apply to pygidia of the Spanish species *Paradoxides mureroensis* Sdzuy (1958 : pl. 1, fig. 13 only; 1961 : pl. 17, figs 1–5) and *Paradoxides* sp. II of Courtessole (1973 : pl. 10, fig. 2) from SW France. Although Šnajdr (1958 : 250) emphasized the long pygidial axis of *Acadoparadoxides* as being distinct from that of *Eccaparadoxides*, some of his illustrations (Šnajdr 1958 : pl. 16, figs 8, 13, 17) of *A. sacheri* show the axis no longer than that of the Turkish material; in others (Šnajdr 1958 : pl. 16, figs 6, 9, 10, 12) the 'axis' apparently combines both axis and pleural fields. The new species is more closely related to *Acadoparadoxides* than to *Paradoxides* (s.s.), and the proportionately longer pygidium of *P. paradoxissimus* (Wahlenberg, 1821) (Westergård 1953 : pl. 8, fig. 2) has the well-segmented axis clearly separate from almost flat pleural regions.

No intermediate forms have been found linking the type and other pygidia with It.2159 (Fig. 26), referred questionably to *P.* (s.l.) *pentagonalis*, in which the tip is squarely truncated. Pygidia from Comley, Shropshire, illustrated by Cobbold (1911: pl. 24, figs 6, 7) also have the tip square in outline but are otherwise quite different.

? Family **ORDOSIIDAE** Lu, 1954

Genus ***CHELIDONOCEPHALUS*** King, 1937

TYPE SPECIES. By original designation, *C. alifrons* King, 1937.

The resemblance of the frontal area of the cranidium of *Chelidonocephalus* to that of *Poshania* Chang, noted by Chang (1959 : 223) and, more particularly, by Fortey & Rushton (1976 : 335), forms the basis of the present discussion. *Poshania* as first used by Chang (1957 : 15, 19–21, 29, 31; pl. 1, fig. 4) was invalid because no generic diagnosis was given; *Poshania Poshanensis*, from the Middle Cambrian of Shantung, which was illustrated by means of a line drawing, was apparently the type species by monotypy but not diagnosed or described. Subsequently the genus was both diagnosed and described, with *P. poshanensis* as type species, by Chang (1959 : 200–203, 221–223; pl. 2, figs 4–10; text-fig. 21); he considered *Poshania, Namanoia* Lermontova, 1951, *Ordosia* Lu, 1954 and *Taitzuia* Resser & Endo, 1935 to belong to the same family, for which he suggested Namanoiidae Lermontova, 1951. Fortey & Rushton (1976 : 335), in seeking an appropriate family for *Chelidonocephalus*, considered both Namanoiidae and the superfamily Rhyssometopacea Öpik (1967 : 272) ineligible. In the meantime Chang (1963 : 475) assigned *Poshania, Ordosia, Taitzuia, Parataitzuia* Chang, 1963, *Tylotaitzuia* Chang, 1963, *Inouyella* Resser & Endo, 1937 and *Peichiashania* Chang, 1959 to the Subfamily Ordosiinae of the Family Ordosiidae, a group proposed originally by Lu (1954 : 435) as a monogeneric subfamily of the Family Leiostegiidae Bradley, 1925. The same classification was followed by Lu *et al.* (1965 : 219 *et seqq.*).

The type species of *Ordosia*, *O. fimbricauda* Lu (1954 : 422, 436; pl. 1, figs 12–18; see also Lu *et al.* 1965 : 220; pl. 38, figs 8, 9), from the Kushan Formation of Manchuria and Inner Mongolia, was founded in part on incomplete cranidia with subparallel glabellar outline, a very short (sag.) anterior border, and a poorly-defined area in front of the glabella which may indicate the presence of a plectrum. Based on an incomplete cranidium refigured by Lu *et al.*

(1965 : 221; pl. 38, fig. 10), the type of species of *Taitzuia, T. insueta* Resser & Endo *in* Kobayashi, 1935, is seen to have very wide fixigenae (*c.* two-thirds the adjacent width of the glabella) and the anterior border close to the frontal lobe, with no indication of a plectrum. Other species of *Taitzuia* have been described and of these *T. glabella* Endo, 1944 and *T. lui* Chu, 1960 (see Lu *et al.* 1965 : pl. 38, figs 14–19) have a glabellar outline and eye ridges like *Chelidonocephalus* and *Derikaspis*, and possibly a median plectrum, though this is less clear. *Poshania poshanensis* and *P. transversa* Chang (1959 : pl. 2, figs 11, 12), though resembling *Chelidonocephalus* and *Derikaspis* in glabellar outline and in the development of eye ridges, plectrum and true border furrow, differ in having a much shorter (sag.) anterior border and no false border furrow. On the other hand *Poshania liaotungensis* (Endo, 1944), *P. obscura* (Walcott, 1905) and *P. tungshanensis* Chang *in* Lu *et al.* 1965 (see Lu *et al.* 1965: pl. 39, figs 12–14, 17, 18) have a longer anterior border than *P. poshanensis*, and probably also a plectrum and traces of a false border furrow. According to Lu *et al.* (1979 : 30), *Poshania* occurs only in the *Taitzuia* Zone, immediately below the *Damesella* Zone, highest subdivision of the Middle Cambrian in China.

The relationship of *Chelidonocephalus* and *Derikaspis* to *Poshania* appears acceptable, but that to *Ordosia* and *Taitzuia* is less obvious and for the present they are referred only questionably to the Ordosiidae. The Family Tengfengiidae Chang, 1963, founded on *Tengfengia latilimbata* Hsiang, 1962 (Lu *et al.* 1965 : 148; pl. 24, figs 9, 10; misspelt as *Tenfengia latelimbata* on p. 763 – see also *T.* cf. *latilimbata* of Chang, 1963: pl. 1, fig 8) is considered inappropriate as there are four pairs of glabellar furrows, the glabellar outline expands in front of the 3p glabellar lobes, the preglabellar field is very wide (exsag.), equal to about half the glabellar length, and there is no clear evidence of a plectrum.

Chelidonocephalus anatolicus sp. nov.

Figs 37–42, ?Figs 45–49

DIAGNOSIS. *Chelidonocephalus* species with broad (sag.) to very broad, flat anterior border and smooth exoskeletal surface. Anterior border furrow incised distally but shallowing rapidly, becoming indiscernible medially, immediately in front of narrow (sag.), subelliptical plectrum. Pair of elongated (tr.) anterior pits sited in preglabellar furrow, near anterolateral angles of frontal glabellar lobe which may show incipient bilobation. Glabella trapezoidal in outline; in some instances a low median ridge and traces of two or three pairs of lateral glabellar furrows may be present, those of the 1p pair being bifurcate. Palpebral lobes set moderately close to glabella and a short distance in front of posterior border. Low but distinct eye ridges traverse axial furrows to join sides of frontal glabellar lobe. Well-developed occipital ring has median tubercle set well back. Lateral and posterior border furrows join to form single, shallow furrow which extends along stout, moderately long librigenal spine.

HOLOTYPE. It.3372 (Figs 37a–c).

OTHER MATERIAL. It.3374 (Fig. 42), It.3388 (Figs 39a, b), It.3389 (Fig. 40), It.3407 (Fig. 41), MTA coll. unnumbered (Fig. 38); also 39 mostly fragmentary specimens (32 of them small cranidia) from S.4; 34 (23 of them cranidia) from S.7; 7 from S.8; 5 from S.9; and 4 from S.11. Two hypostomata, It.3390 (Fig. 46) and It.3409 (Figs 47a, b) from loc. S.7 are assigned questionably to *C. anatolicus*. For an account of the pygidia, see discussion of *Derikaspis toluni*.

LOCALITIES AND HORIZONS. The holotype is from loc. S.4, and the other specimens are from locs S.7–S.9 and S.11. These localities lie from 80 m to about 182 m above the base of the Sosink Formation.

DIMENSIONS (in mm).	It.3372	It.3388	It.3389	MTA Coll.
Median length of cranidium	8·4	10·2	4·7	9·9
Basal breadth of cranidium	11·3*	14·0*	–	14·2*
Median length of glabella and occipital ring	5·5	6·4	3·2	6·6
Basal breadth of glabella	3·7	5·1	2·4	4·8
Breadth of frontal area	7·7	–	4·2	9·0
Distance across palpebral lobes	8·8*	–	5·4*	10·6

DESCRIPTION AND DISCUSSION. The type and one other species of *Chelidonocephalus* from Iran were described by Fortey & Rushton (1976: 336), whose material has much in common with the new Turkish species; it is preferred to indicate the salient features of the latter rather than give a largely repetitive description. The most conspicuous feature of the cranidium of *C. anatolicus* is the large, brim-like structure formed mainly by the very long (sag.) anterior border, which carries a broad (sag.), shallow and often ill-defined false border furrow. The incised anterior border furrow runs from the sides of the cranidium in a broad arc, but its median half is either effaced or indicated by a subtle change in slope, immediately behind which is the median plectrum. The latter forms a narrow (sag.), subelliptical strip which may be clearly visible (Fig. 39b), though never strongly defined, but which may be almost indistinguishable (Fig. 38). A small, immature cranidium (Fig. 40) has three distinct pairs of lateral glabellar lobes, the false border furrow is relatively deep, the anterior border is short and the abaxial portions of the border furrow are distinct. In the largest cranidium (Fig. 42) the anterior border is remarkably long and of scoop-like form owing to widening (sag.) of the false border furrow; the anterior border furrow is shallow, broad (exs.), and dies out adaxially, being replaced by a low ridge that bounds the front of the plectrum. All available cranidia, large and small, have low eye ridges which traverse the axial furrows and join the frontal glabellar lobe, where bilobation of an apparent parafrontal band is weakly developed (Figs 37a, 37c, 38, 39b) in line with an indistinct axial ridge. On the adaxial side of each anterolateral angle of the glabella, one of a pair of elongated depressions occurs in the preglabellar furrow. The depressions appear to correspond to anterior pits (or fossulae; Harrington, Moore & Stubblefield *in* Moore, 1959 : O46, O120), but are sited farther forwards on the glabella and behind the lateral extremities of the plectrum. The surface of the exoskeleton is often smooth, or almost so, particularly in the case of larger specimens; fine granulation may be developed, particularly on the glabella, excluding the weakly-developed two or three pairs of glabellar furrows, which are not incised.

The similarity of *Chelidonocephalus anatolicus* to the Iranian *C. alifrons* King (1937 : 17; pl. 2, figs 8a–d), redescribed by Fortey & Rushton (1976 : 336), and *C. preannulatus* Fortey & Rushton (1976 : 338) is evident. The cranidium of *C. alifrons* may be distinguished from

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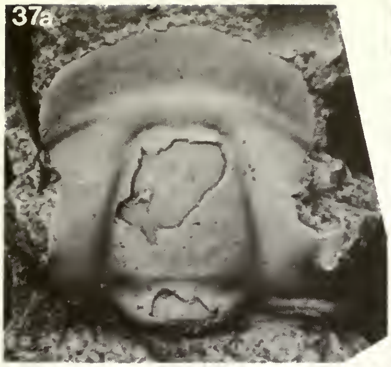
Figs 37–42 *Chelidonocephalus anatolicus* sp. nov. Figs 37a–c, dorsal, oblique left lateral and anterior views of almost complete cranidium. **Holotype**, It.3372, × 5. Loc. S.4. Fig 38, incomplete cranidium showing outline of palpebral lobe. MTA coll., unnumbered, × 4. Loc. S.7. Figs 39a, b, right lateral and dorsal views of incomplete large cranidium showing parafrontal band and very long anterior border. It.3388, × 5. Loc. S.4. Fig. 40, small cranidium with relatively long (sag.) palpebral lobes. Three pairs of lateral glabellar furrows are visible, those of the 1p pair bifurcating adaxially. It.3389, × 7. Loc. S.4. Fig. 41, left librigena. It.3407, × 8. Loc. S.7. Fig. 42, latex cast of fragment of largest available cranidium, with very long, flat border. Eye ridges are distinct, but median plectrum is little more than a wide (sag.) median depression in front of the glabella, and anterior border furrow and false border furrow are much reduced. It.3374, × 2·5. Loc. S.4. See also Figs 45–49.

Figs 43–44 *Chelidonocephalus* sp. Loc. S.15. Figs 43a, b, dorsal and anterior views of incomplete exfoliated cranidium. It.2139, × 6. Fig. 44, incomplete large cranidium in which anterior border is relatively short (sag.); eye ridges, parafrontal band and glabellar furrows are almost indiscernible. It.2128, × 7.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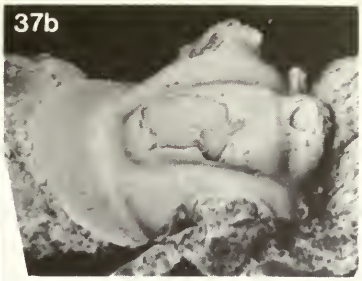
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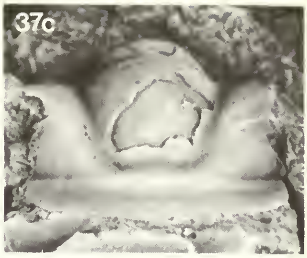
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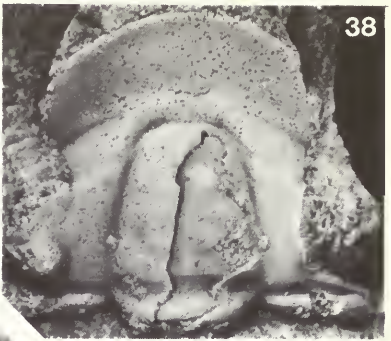
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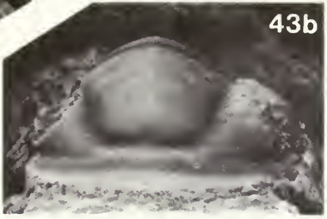
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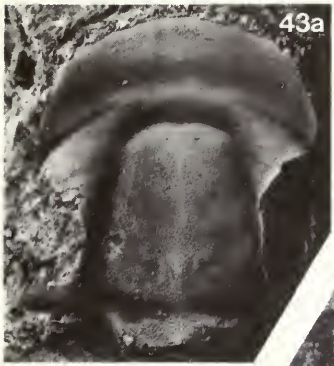
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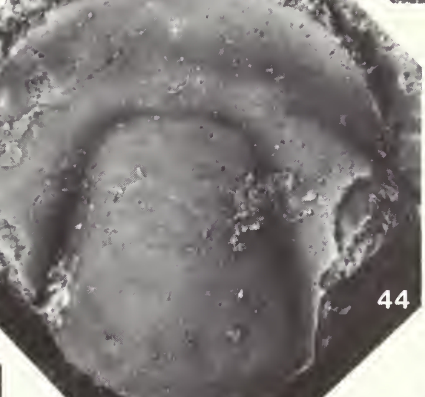
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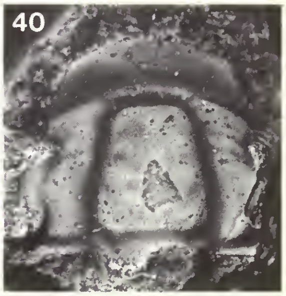
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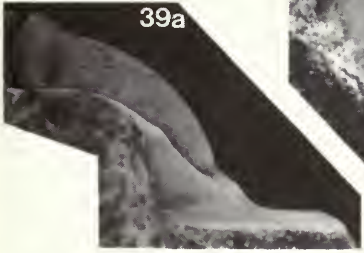
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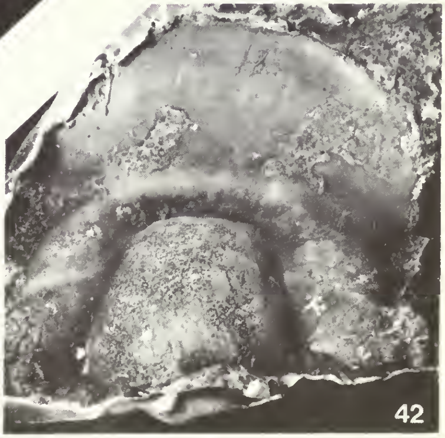
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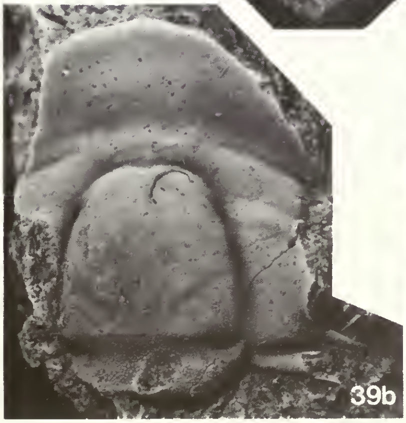
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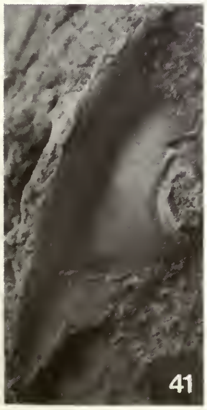
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C. anatolicus by its wider fixigenae, with eyes set farther forwards, and longer (tr.) incised portions of the border furrow. The median length of the frontal area is approximately one-third of the cranidium in the holotypes of *C. anatolicus* and of *C. alifrons*, but is proportionately greater in larger cranidia of *C. alifrons* as shown in Figs 39b and, particularly 42. The parafrontal lobe and plectrum are of similar size and development in both species, but the rearward curvature of the border furrow to the outer ends of the plectrum in *C. alifrons* has not been demonstrated in *C. anatolicus. Chelidonocephalus preannulatus* has a shorter anterior border and longer palpebral lobes than *C. anatolicus*, and the front of the glabella is proportionately narrower (tr.); as in *C. alifrons*, the backward curve of the border furrow to the preglabellar furrow is clearly seen.

The hypostoma of the type species of *Chelidonocephalus, C. alifrons,* has not been described; a single example attributed to *C. preannulatus* Fortey & Rushton (1976 : 338; pl. 9 figs 3, 4) is very different from the Derik material and is not congeneric. The Iranian specimen lacks posterior wings, the rim-like lateral and posterior borders are continuous, the anterior wings are long (tr.) and pointed and the middle furrow is set just behind the centre of the hypostoma. A small hypostoma attributed to *Koldiniella mitrella* Sivov, 1955 by Fortey & Rushton (1976 : pl. 10, fig. 16), though incomplete frontally, more resembles that of *Chelidonocephalus* as interpreted from the Derik material, but the posterior lobe of the middle body is proportionately larger.

For an account of pygidia assigned questionably to *Chelidonocephalus anatolicus*, see discussion of *Derikaspis toluni* (p. 31).

Chelidonocephalus sp.

Figs 43a, b, 44

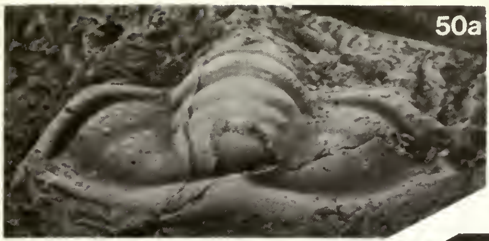
Figured material. It.2128 (Fig. 44), It.2139 (Figs 43a, b).

Horizon and locality. 190 m above the base of the Sosink Formation, at loc. S.15.

Description and discussion. One of two figured cranidia (Fig. 44), with median length of 8 mm*, has the anterior border proportionately shorter than that of *Chelidonocephalus anatolicus* (estimated 22% of median length compared with 28%); the false border furrow, eye ridges, parafrontal lobe, median plectrum and anterior pits are more weakly developed or almost indiscernible. These features are most distinct on a slightly larger cranidium (Figs 43a, b) which shows, in addition, bilobation of the frontal glabellar lobe, traces of a low median ridge on the glabella, a distinct occipital tubercle, bifurcating but very shallow 1p glabellar furrows and an incised, relatively long (tr.) border furrow which extends adaxially until almost in line with the axial furrows. In both specimens the surface of the exoskeleton is ornamented, at least in part, with fine granules. Coarser granulation covers most of the glabella of *Chelidonocephalus preannulatus* Fortey & Rushton (1976 : 338) from Iran, a species which differs also in having the plectrum better defined, particularly laterally, and a more tapered glabellar outline.

Figs 45–49 ? *Chelidonocephalus anatolicus* sp. nov. Figs 45a, b, dorsal and posterior views of partially exfoliated pygidium. It.2294, × 3. Loc. S.2. Fig. 46, incomplete hypostoma. It.3390, × 8. Loc. S.7. Figs 47a, b, lateral and posterior views of incomplete hypostoma. It.3409, × 8. Loc. S.7. Fig. 48, small pygidium. It.3402, × 20. Loc. S.7. Figs 49a–c, left lateral, dorsal and posterior views of pygidium. It.3405, × 6. Loc. S.4. See also Figs 37–42.

Figs 50–51 ? *Derikaspis toluni* gen. et sp. nov. Figs 50a–c, posterior, left posterolateral and dorsal views of partly exfoliated pygidium. It.3399, × 5. Loc. S.11. Fig. 51, dorsal view of hypostoma showing tubercles on anterior lobe of middle body. It.3370, × 5. Loc. S.4. See also Figs 52–59.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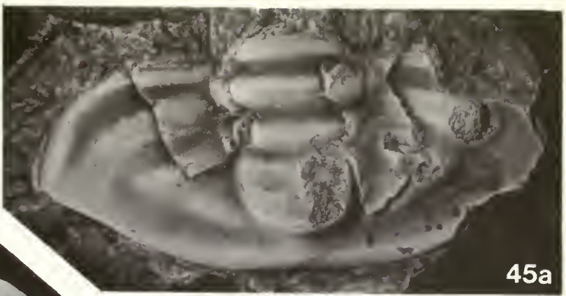
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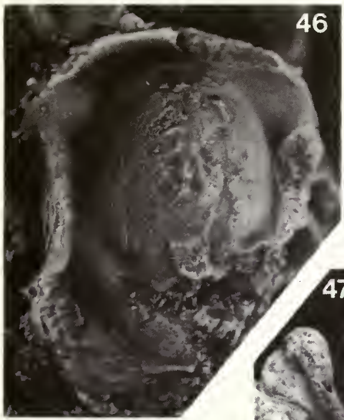
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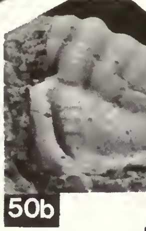
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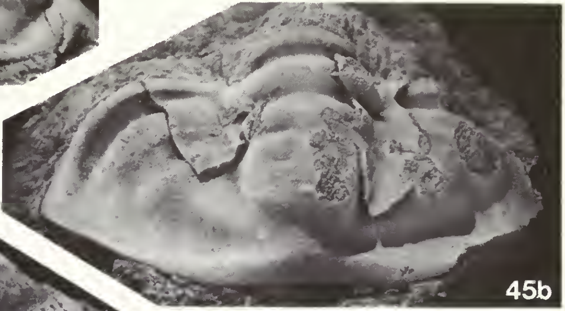
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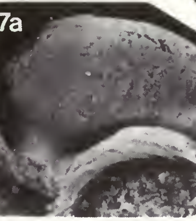
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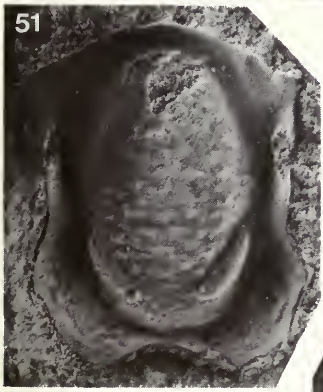
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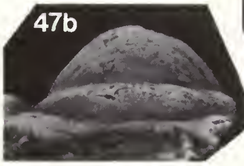
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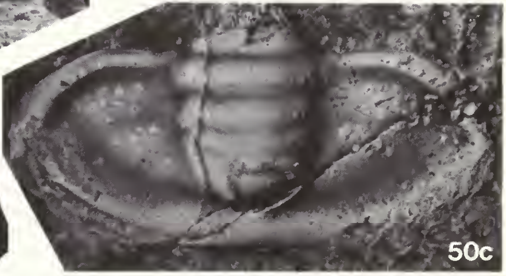
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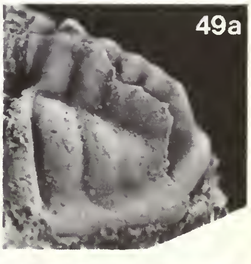
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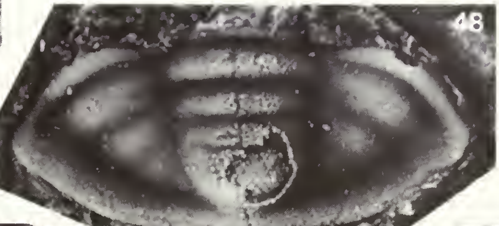
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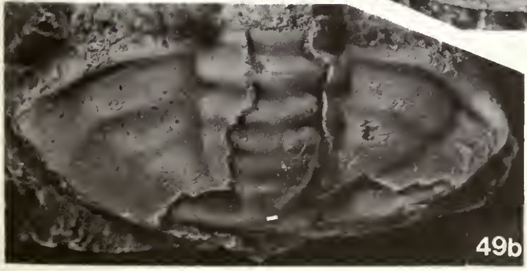
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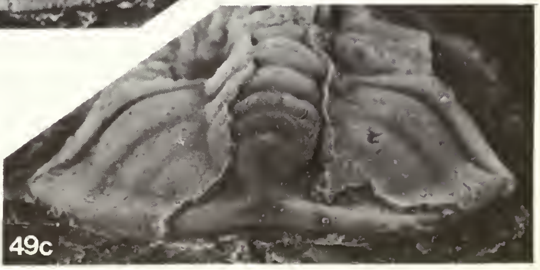

49c

Chelidonocephalus has not been recorded other than from Iran and SE Turkey but may be represented in the Montagne Noire, SW France. Undetermined cranidia described by Courtessole (1973: 218; pl. 26, figs 8–11) from Niveaux H and I (highest Middle Cambrian of that region), though tectonically deformed, appear to show the salient features of the genus, including true and false border furrows and, possibly, a plectrum.

Genus ***DERIKASPIS*** nov.

Diagnosis. Glabellar outline subtrapezoidal, moderately tapered anteriorly where frontal glabellar lobe is slightly bilobed and includes poorly-defined parafrontal band. Conspicuous, high palpebral lobes, set behind centre with reference to glabella, are linked to frontal glabellar lobe by distinct, straight eye ridges. Median tubercle on occipital ring. Occipital furrow deepest abaxially. 1p and 2p lateral glabellar furrows very shallow, the 1p furrows bifurcating adaxially to delimit pair of large, intermediate lobes; 3p furrows absent or suggested by traces immediately behind the eye ridges. Incised anterior border furrow developed only abaxially, behind broad (sag.), shallow, false border furrow; remainder of anterior border forms wide (sag.), flat brim. Pair of long (tr.) anterior pits sited abaxially in preglabellar furrow and behind extremities of subelliptical median plectrum, which may be moderately defined or almost indistinguishable. Surface of cranidium ornamented with variable combination of granules and tubercles of different sizes.

Type species. *Derikaspis toluni* sp. nov.

Other species. *Jincella*? *brianensis* Courtessole, 1973.

Distribution. Middle Cambrian, SE Turkey and SW France.

Derikaspis toluni sp. nov.

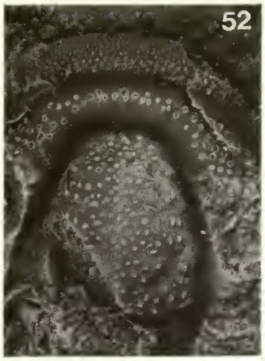
Figs 52–59, ?Figs 50–51

Holotype. It.3363 (Figs 53a–c).

Other material. It.1171 (Fig. 55), It.3391 (Fig. 59), It.3392 (Fig. 52), It.3393 (Fig. 56), It.3396 (Fig. 54), It.3408 (Fig. 57), MTA coll. unnumbered (Figs 58a–c). Also 13 specimens (11 cranidia) from S.1, 25 specimens (18 cranidia) from S.2, 29 specimens (16 cranidia) from S.3, 17 specimens (13 cranidia) from S.4, 16 specimens (7 cranidia) from S.5, 2 cranidia from S.10, 13 specimens (6 cranidia) from S.11, 22 specimens (18 cranidia) from S.12, one fragment of cranidium and two of librigenae from S.13 and two fragments of cranidium from S.16; most of the above unfigured material is incomplete. Pygidium It.3399 (Figs 50a–c) and hypostoma It.3370 (Fig. 51) are referred questionably to the species.

Horizons and localities. *Derikaspis toluni* was found at locs S.1, S.2, S.3, S.4 and S.5 in the area NW of Sosink, and at S.10, S.11, S.12, S.13 and S.16 in the stream valley north of the village. Stratigraphically these range from 18 m to 225 m above the base of the Sosink Formation. The holotype is from S.3.

Figs 52–59 *Derikaspis toluni* gen. et sp. nov. Fig. 52, incomplete cranidium ornamented with coarse tubercles. Note slightly larger tubercles on frontal glabellar lobe. It.3392, × 3. Loc. S.11. Figs 53a–c, dorsal, anterior and oblique right lateral views of cranidium. Note reduction in ornamentation behind eye ridges. **Holotype**, It.3363, × 4. Loc. S.3. Fig. 54, part of right librigena showing librigenal spine and granulose surface. It.3396, × 3. Loc. S.12. Fig. 55, incomplete, almost exfoliated, large cranidium. It.1171, × 2·5. Loc. S.12. Fig. 56, fragmentary cranidium exhibiting distinct parafrontal band. It.3393, × 2. Loc. S.2. Fig. 57, large right librigena with strongly ornamented surface. It.3408, × 3. Loc. S.12. Figs 58a–c, oblique left lateral, dorsal and anterior views of small cranidium with well-developed ornamentation of tubercles. MTA coll., unnumbered, × 4·5. Loc. S.3. Fig. 59, incomplete large cranidium showing adaxial bifurcation of 1p glabellar furrows to encompass intermediate glabellar lobes. The distinctly individual ornamentation of the frontal glabellar lobe behind the line of the eye ridges, and its incipient bilobation immediately behind the parafrontal band, are clearly visible. It.3391, × 3. Loc. S.11.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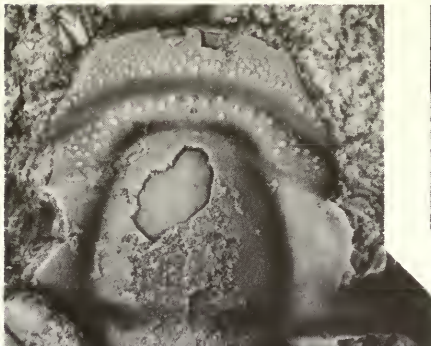
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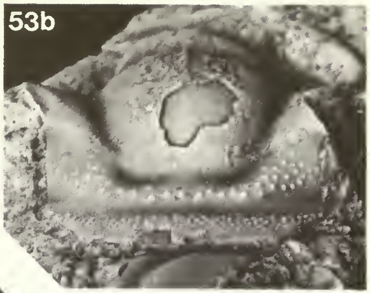
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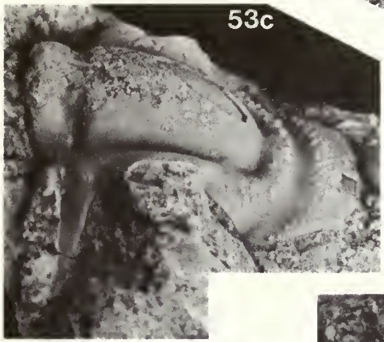
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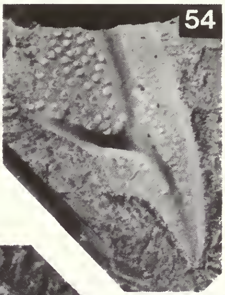
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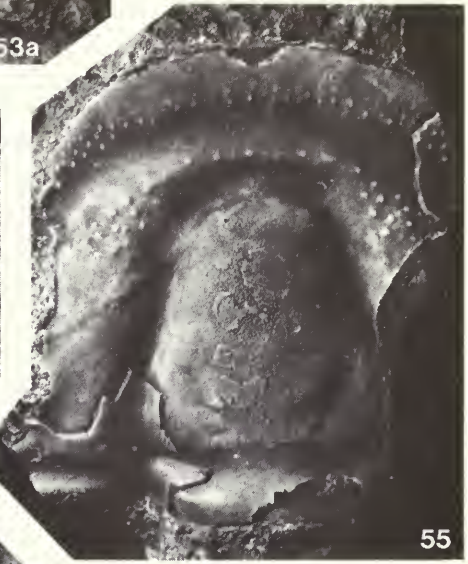
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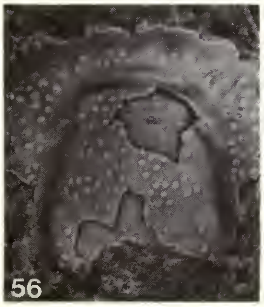
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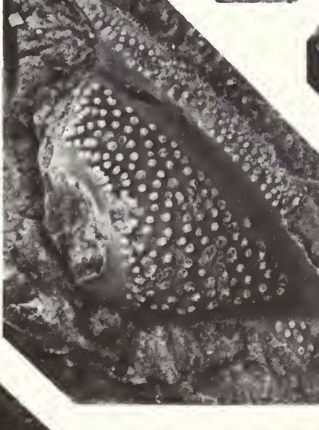
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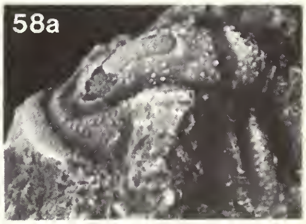
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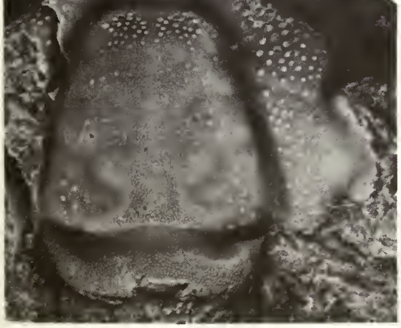
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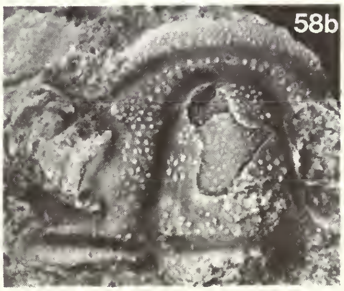
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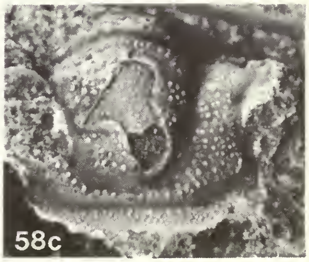

58c

Dimensions (in mm).	It.3363	It.1171	It.3391	MTA Coll.
Median length of cranidium	11·7	24·5	–	7·6
Basal breadth of cranidium	17·4*	–	–	12·5
Median length of glabella and occipital ring	16·2	17·3	12·7	5·6
Basal breadth of glabella	6·1	12·7	9·5	4·0
Maximum breadth of frontal area	9·3	23·2*	15·3*	6·2
Distance across palpebral lobes	12·0*	–	20·8*	9·4*

Description and discussion. The new genus is apparently closely related to *Chelidonocephalus*, and features common to both include bifurcate 1p lateral glabellar furrows, eye ridges and poorly-defined parafrontal lobe, border furrow deepest abaxially and a false border furrow. *Derikaspis* is distinguished as follows. The surface of small cranidia is always ornamented with tubercles while that of large specimens may be all or partly tuberculate, but is never totally smooth or finely granulate as in *Chelidonocephalus*. The false border furrow is well defined and deep, whereas in *Chelidonocephalus* it is shallow and may be indistinct; the anterior border is consistently shorter (sag.) at all stages of development, and particularly so in large cranidia. Well-developed intermediate lobes like those of *Derikaspis* are also found in *Iranoleesia pisiformis* (King, 1937) (see Fortey & Rushton 1976 : esp. pl. 9, figs 8, 9); they are present but much less evident in *Chelidonocephalus*.

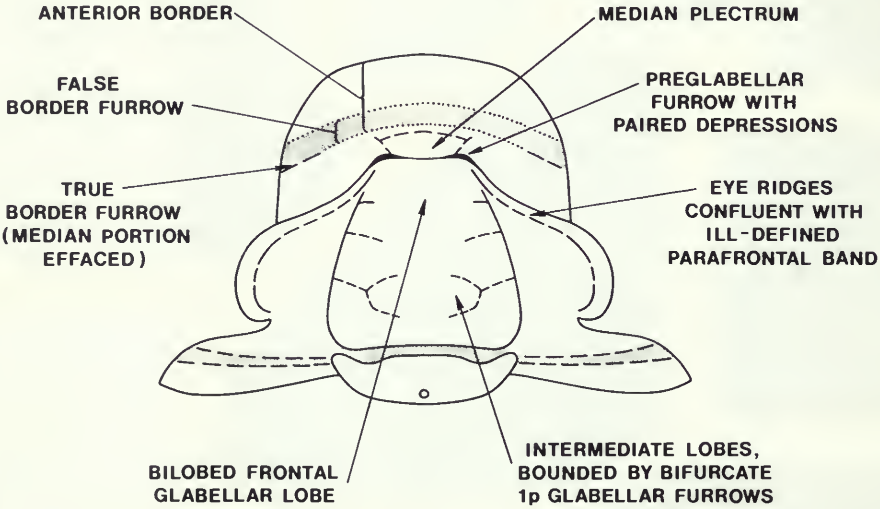

ANTERIOR BORDER
MEDIAN PLECTRUM
FALSE BORDER FURROW
PREGLABELLAR FURROW WITH PAIRED DEPRESSIONS
TRUE BORDER FURROW (MEDIAN PORTION EFFACED)
EYE RIDGES CONFLUENT WITH ILL-DEFINED PARAFRONTAL BAND
BILOBED FRONTAL GLABELLAR LOBE
INTERMEDIATE LOBES, BOUNDED BY BIFURCATE 1p GLABELLAR FURROWS

Fig. 60 Outline drawing of cranidium of *Derikaspis toluni* gen. et sp. nov., showing structural elements discussed in text. Ornamentation omitted.

Librigenae of *Chelidonocephalus anatolicus* and *Derikaspis toluni* are closely similar in shape, and in all cases the lateral and posterior border furrows join at the genal angle to form a single furrow that dies out along the librigenal spine. Those of *C. anatolicus* invariably have a smooth surface but in the case of *D. toluni* the genal field (Fig. 57) is ornamented with coarse tubercles, though these are sometimes less well developed, while the lateral border carries small tubercles that become still smaller towards the margin. Associated hypostomata and pygidia of the two species are also remarkably alike, and for the present are separated mainly on the basis of the ornamentation, those with a tuberculate surface being assigned to *D. toluni*. Evidence of the hypostoma is sparse, but a well-preserved specimen assigned questionably to *D. toluni* (Fig. 51) has the coarsely tuberculate middle body proportionately narrower and more tapered frontally than in examples (Figs 46, 47a, b) referred, also questionably, to *C. anatolicus*. All these have in common the anterior border rim-like medially, dying out abaxially; the lateral border rim-like, subparallel opposite centre of hypostoma but dying out frontally towards pair of short (tr.), triangular, anterior wings and posteriorly to a large pair of posterior wings that are obliquely truncated posterolaterally; a broadly rounded median notch indenting the posterior margin; and the middle body divided by a shallow, parabolic middle furrow into two markedly unequal lobes, the posterior of which is the smaller and carries traces of a pair of maculae.

Pygidia assigned questionably to the two species are more than twice as broad as long, with outline rounded posteriorly. Pleural fields are convex, declining steeply to the ill-defined border, bounded by a shallow border furrow that becomes still shallower at the axial line. The clearly differentiated anterior half ribs, transversely straight near the axial furrows but curving backwards abaxially and truncated by a pair of articulating facets, are followed by two weakly-defined pairs of ribs; the subparallel pleural furrows become markedly shallower outside the pleural fields. The prominent, straight-sided, slightly tapered axis has a frontal breadth about one-third, or slightly less, that of pygidium. There are three or four transversely straight axial rings, the first two of which are most clearly defined, and on internal moulds (Figs 45a, 49c) the small terminal piece is seen linked by a very short postaxial ridge to the medially thickened border. Two pygidia from the Mila Formation attributed by Fortey & Rushton (1976 : pl. 9, figs 7, 11) to *Chelidonocephalus preannulatus* and, possibly, *C. alifrons* do not belong with *Chelidonocephalus* if the Turkish material is correctly interpreted. The Iranian specimens, though incomplete, are proportionately longer, have more axial rings and a less well defined terminal piece, and the border appears to be broader and flatter.

The other known occurrence of *Derikaspis* is in Niveau H of the Montagne Noire, SW France, where *Jincella* ? *brianensis* Courtessole (1973 : 174; pl. 17, figs 2–4) is considered here to be congeneric with *D. toluni*. Courtessole's specimens are most closely comparable with a much smaller Turkish specimen (Figs 58a–c) but have wider fixigenae, a larger development of tubercles in front of the furrow representing the plectrum, and apparently less well developed anterior pits. In larger cranidia the differences are considerable; compare Fig. 55, 24·5 mm long, with Courtessole's pl. 17, fig 3, *c*. 21 mm long. *D. toluni* exhibits much reduced ornamentation of both glabella and fixigenae, a wider (sag.) false border furrow, a shorter (sag.) anterior border and weaker glabellar furrows.

Family **ANDRARINIDAE** Raymond, 1937

Genus ***HOLASAPHUS*** Matthew, 1895

TYPE SPECIES. By monotypy, *Holasaphus centropyge* Matthew, 1895.

Holasaphus mesopotamicus Dean, 1972

1972 *Holasaphus mesopotamicus* Dean: 274; pl. 1, fig. 7; pl. 11, figs 1–7.

Although not refigured in the present account, the species is included because the type material came from the Sosink Formation in the area north of Sosink. The horizon was estimated to lie some 500 m above the base of the Sosink Formation as interpreted by Kellogg (1960) and the occurrence is therefore relevant to an assessment of the formation's age.

Holasaphus has, as yet, been reported from only two regions. In its type area of Cape Breton Island, Nova Scotia, eastern Canada, *H. centropyge* (see accounts by Hutchinson 1952 : 25, 26, 104; Dean 1972 : 274) was found in strata containing *Paradoxides abenacus* Matthew, 1886, a species stated by Hutchinson to be indicative of the *Paradoxides hicksii* Zone, approximately in the middle part of the Middle Cambrian (Cowie *et al.* 1972 : 10; pl.

5). *Holasaphus mesopotamicus* is an apparently younger species and its age, judged on that of the trilobites in the lowest Sosink Formation, is probably late Middle Cambrian.

Howell (*in* Moore 1959 : O261) placed *Holasaphus* in the Andrarinidae. The type species of *Andrarina, A. costata* (Angelin, 1854), was redescribed by Westergård (1948 : 14) and is characteristic of, though uncommon in, the *Lejopyge laevigata* Zone, highest Middle Cambrian, of Sweden. A cranidium preserved in shale from eastern Newfoundland and illustrated by Poulsen & Anderson (1975 : 2071; pl. 1, fig. 1) strongly resembles *H. mesopotamicus* and may be of broadly comparable age.

Family uncertain

Genus & species **undetermined A**

Figs 64a–c, ?65

FIGURED SPECIMENS. It.3378 (Figs 64a–c) from loc. S.7, 135 m above the base of the Sosink Formation. It.2121 (Fig. 65), from loc. S.11, 90 m above the base of the Sosink Formation, is referred questionably to the same form.

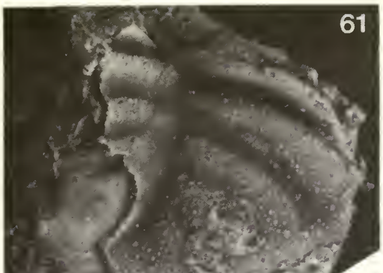
DIMENSIONS. It.3378: Median length of cranidium 6 mm*, overall breadth of cranidium 8·3 mm, median length of combined glabella and occipital ring 4·3 mm*, basal breadth of glabella 3·1 mm, distance across palpebral lobes 6·5 mm*.

DESCRIPTION AND DISCUSSION. The cranidium is of low convexity, both longitudinally and transversely, with approximately three-quarters of the median length occupied by the combined glabella and occipital ring. The glabellar outline is trapezoidal, with straight lateral and frontal margins, and low axial ridge. Three unequal pairs of poorly-defined glabellar lobes are present. The low but conspicuous anterior border has a well-rounded outline and is widest (sag.) medially, where it occupies one-sixth of the cranidial length. The flat preglabellar field is half as wide (sag.) as the anterior border. Small palpebral lobes are set behind the centre with reference to the glabella. A spine base is possibly present on the occipital ring. Most of the surface of the exoskeleton is ornamented with conspicuous, small, closely-spaced pits. Pits are absent from both the axial furrows and the otherwise almost indistinguishable glabellar furrows; they are present on the posterior half of the anterior border but die out frontally, where the intervening areas fuse to produce low, anastomosing ridges subparallel to the margin. The low axial ridge of the glabella is traversed by pitting and is sited in line with a slight shallowing of the preglabellar furrow; the preglabellar field shows traces of low, scattered tubercles, but no pits. The surface of the surviving right palpebral lobe is pitted and almost level with that of the adjacent fixigena. The anterior branches of the facial suture diverge gently forwards to cut the border furrow and then curve adaxially to meet the anterior margin approximately in line with the axial furrows; the posterior branches curve backwards more strongly near the posterior margin.

Figs 61–63 *Conocoryphe* (s.l.) sp. Fig. 61, fragmentary pygidium. It.1148, × 4. Loc. S.5. Figs 62a, b, right lateral and dorsal views of small pygidium. It.1144, × 10. Loc. S.1. Figs 63a–c, left lateral, posterior and dorsal views of partly exfoliated pygidium. It.3403, × 5. Loc. S.13. See p. 12.

Figs 64–65 Genus & species undetermined A. Figs 64a–c, anterior, left lateral and dorsal views of cranidium. It.3378, × 7. Loc. S.7. Fig. 65, incomplete cranidium referred questionably to species. Specimen tilted backwards slightly to show axial ridge on glabella. It.2121, × 10. Loc. S.11.

Figs 66–67 Genus & species undetermined B. Fig. 66, incomplete slightly broken cranidium. It.3371, × 8. Loc. S.4. Figs 67a–c, anterior, dorsal and oblique left lateral views of incomplete cranidium. It.3376, × 7. Loc. S.7.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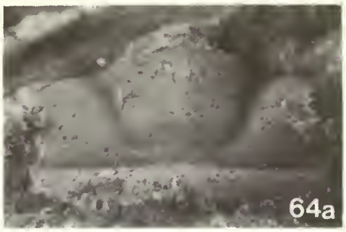
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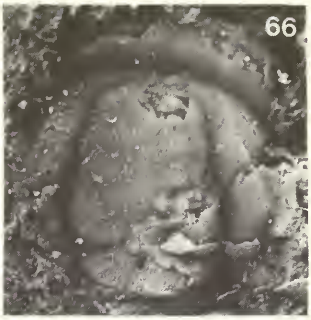
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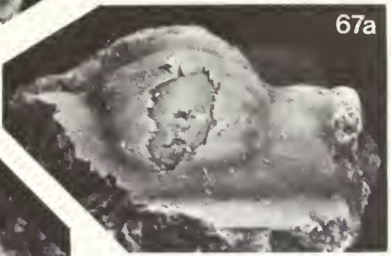
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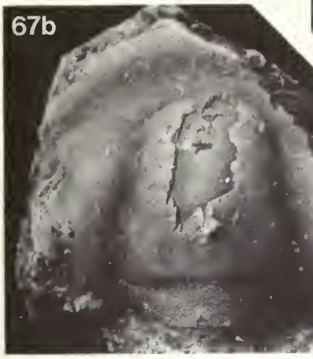
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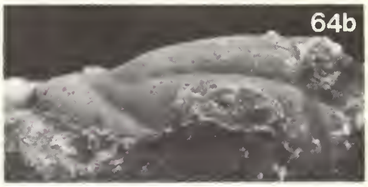
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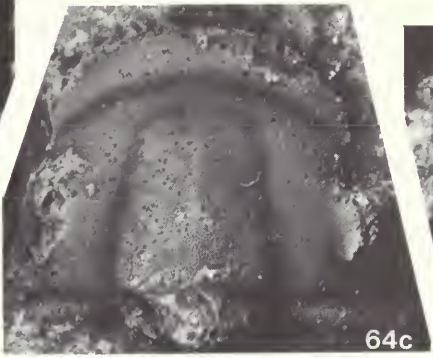
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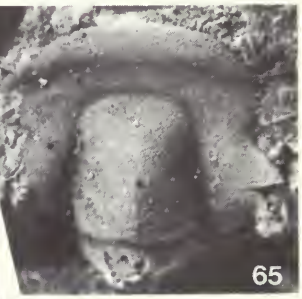
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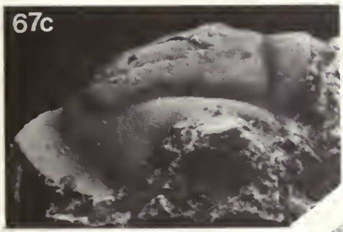
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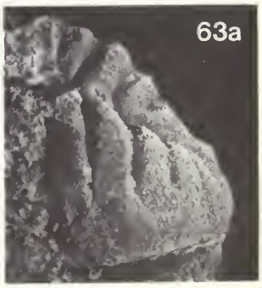
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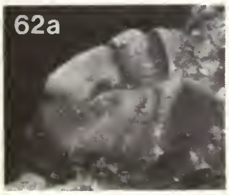
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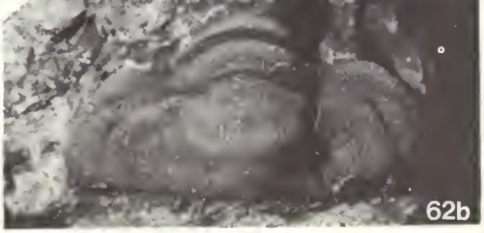
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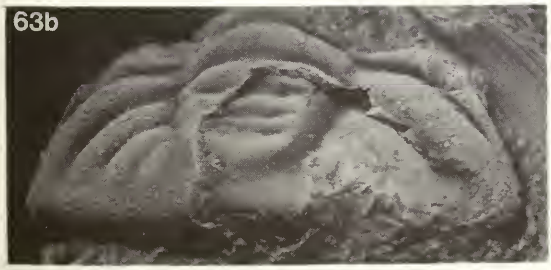
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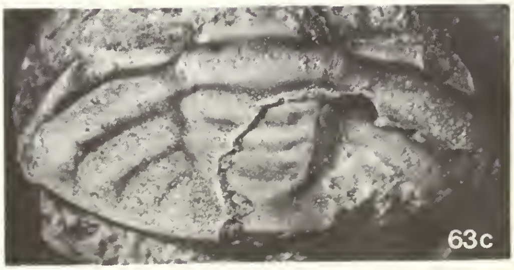
63c

No satisfactory assignment of this material has yet proved possible but a general comparison may be made with the type species of *Manchuriella* Resser & Endo, *M. typa* Resser & Endo (1937 : 241; pl. 36, figs 3–8) from the Middle Cambrian of Manchuria, redescribed by Lu *et al.* (1965 : 298; pl. 53 figs 5–7) and assigned to the Proasaphiscidae. Comparison may particularly be made with Resser & Endo's 1937: pl. 36, figs 3, 5; their description noted the presence of three pairs of shallow lateral furrows and a longitudinal ridge on the glabella. The exoskeleton of the Chinese species was said to be smooth, apart from an occipital node which cannot be satisfactorily demonstrated on the incomplete occipital ring of the present specimen. Other features distinguishing the Turkish species from *Manchuriella typa* are the longer (sag.) anterior border, shorter (sag.) preglabellar field, and narrower (tr.) fixigenae.

A small cranidium, It.2121 (Fig. 65), resembles It.3378 in the form of the anterior border and preglabellar field, the glabellar outline, and the divergent anterior branches of the facial suture; there is a suggestion of an axial ridge. On the other hand the glabella is proportionately shorter and more convex, the anterior border is thicker and less arched in outline, the palpebral lobes are larger, and there is no evidence of ornamentation. The specimen is referred only questionably to the same genus and species.

Genus & species **undetermined B**

Figs 66, 67a–c

Figured specimens. It.3371 (Fig. 66), from loc. S.4; It.3376 (Figs 67a–c) from loc. S.7. The stratigraphic horizons are, respectively, 80 m and 135 m above the base of the Sosink Formation.

Description and discussion. The two fragmentary cranidia have a glabellar outline which tapers gently to the rounded frontal glabellar lobe. Short palpebral lobes are set moderately close to the glabella and the anterior branches of the facial suture diverge to cut, at points longitudinally in line with the palpebral lobes, an anterior border that is low in profile, broadly rounded in plan, and separated from the glabella by a narrow (sag.), flat, preglabellar field. Three inequisized pairs of glabellar lobes are delimited by shallow lateral glabellar furrows, the 1p pair of which, in the case of the larger specimen (It.3371), bifurcate adaxially to produce intermediate lobes. The occipital ring narrows (exsag.) distally. Surface, excluding furrows, ornamented with closely-packed, fine granules, some of which are arranged in anastomosing lines.

Some features of the present material are found in three species of *Liostracus* (*Agaso*) described by Cobbold & Pocock (1934 : 359–362) from the *Paradoxides forchhammeri* Grit of the Wrekin district, Shropshire. All the British species have a tapered glabellar outline, a distinct preglabellar field, and an anterior border which may be slightly or strongly rounded in plan view. The sharply-defined, flat anterior border and steeply declined preglabellar field, particularly of the type species *L.* (*A.*) *rushtonensis* Cobbold & Pocock (1934 : pl. 45, fig. 3b), may be compared with Fig. 67c, though the low transverse convexity of the glabella in all the British species differs from that of the Turkish material.

Age and relationships of the trilobites

The affinities of the Sosink Formation's trilobites lie for the most part with SW Europe and the Mediterranean region, but certain genera reflect the proximity of Iranian faunas to the east, though the latter do not include paradoxidids.

The Middle Cambrian of the Montagne Noire, SW France, was divided by Courtessole (1967*a*) into eight parts, termed 'Niveaux', or levels, and designated successively A to H on the basis of the vertical ranges of their contained trilobites. More detailed ranges of genera and species were given later (Courtessole 1973), and a further level, Niveau I, was added, overlain, apparently disconformably, by Tremadocian strata termed Niveau J. The faunas have much in common with those of northern Spain, where Sdzuy (1971) introduced successive 'niveles', or horizons, of *Conocoryphe ovata*, *Acadolenus*, *Badulesia*, *Pardailhania* and *Solenopleuropsis*, followed by a 'Piso sin Solenopleuropsidae'. Vertical ranges of species were given, though no formal zones were designated, and Sdzuy proposed a provisional correlation between the French and Spanish sequences, together with those in Sweden and eastern Newfoundland. Sdzuy (1971: table 2) correlated Courtessole's Niveau A with the topmost quarter of the *Badulesia* horizon and approximately the lower half of the *Pardailhania* horizon; Niveau B was equated with the upper half of the *Pardailhania* horizon and the lowest third of the *Solenopleuropsis* horizon. Courtessole's subsequent work (1973 : table 3) indicates that *Pardailhania* ranges through the whole of Niveau A in the Montagne Noire, where the Middle Cambrian succession is clearly incomplete. *Badulesia*, represented by a single species, *B. granieri* (Thoral), occurs only in the lower half (A_1) of Niveau A and *Solenopleuropsis* extends from the base of Niveau B to the top of Niveau F. Niveaux G to I thus correspond to at least part of Sdzuy's 'Piso sin Solenopleuropsidae'.

Solenopleuropsis marginata marginata from the lowest available fossiliferous level in the Sosink Formation is taken to indicate part of the highest third of the north Spanish *Solenopleuropsis* horizon, in accordance with Sdzuy's (1971: table 1) recorded range of the subspecies there. Although *S. marginata* has not been reported from France, the Sosink record probably corresponds approximately to Niveau F there. It is from Niveaux F and H that the so-called 'oculé' forms of *Conocoryphe* (*Conocoryphe*) are known in the Montagne Noire. In Spain *C.* (*C.*) *sdzuyi* Courtessole (1976*b*) was recorded originally, as *C.* (*C.*) *pseudooculata* Miquel, by Sdzuy (1971 : table 1), from the highest part of the *Solenopleuropsis* horizon and the lowest 'Piso sin Solenopleuropsidae'. All these correspond at least approximately to the occurrence of *C.* (*C.*) *caecigena* within a restricted part (20 m) of the Sosink Formation and the group may have some potential in correlation.

Paradoxides (*Eccaparadoxides*) is widely distributed in the Mediterranean–Bohemian region, and ranges throughout the incomplete Middle Cambrian of the Montagne Noire, where certain species are restricted in their vertical distribution (Courtessole 1973). *P.* (*E.*) *remus* has not yet been found elsewhere but, judged on evidence in the lowest Sosink Formation, may have evolved from the apparently earlier *P.* (*E.*) *pradoanus*, recorded by Sdzuy (1971 : table 1) from the highest third of the *Pardailhania* horizon and lowest two-thirds of the *Solenopleuropsis* horizon in Spain.

Dorypyge is a widespread genus, found mostly in the Middle Cambrian of both China and western Europe, and *D. terneki* contributes little evidence of age, though its resemblance to *D. aenigma* (Linnarsson), from the *Solenopleura brachymetopa* Zone of Sweden, was noted on p. 14. *Peronopsis fallax minor* (Brögger), also described from the Swedish *S. brachymetopa* Zone, may be cited as further evidence of a late Middle Cambrian age, but evidently had an extended vertical range, judged on the record of *P. fallax* cf. *minor* from the *Agnostus pisiformis* Zone, lowest Upper Cambrian, of central England (Taylor & Rushton 1972 : 19).

Chelidonocephalus is known elsewhere only from Iran, where a recent revision by Fortey & Rushton (1976) assigned *C. alifrons* King, 1937 to the *Dorypyge* Zone, highest subdivision of the Iranian Middle Cambrian as interpreted by Kushan (1973 : 125). The succeeding *Drepanura* Zone was said to contain, *inter alia*, *Koldiniella mitella* Sivov, 1955, indicative of lowest Upper Cambrian, *Chelidonocephalus preannulatus* Fortey & Rushton (1976 : 338) and an unnamed species of *Dorypyge*, in this instance ranging upwards from its named zone. The occurrence near Sosink of *Chelidonocephalus* with and above *Solenopleuropsis* predates that in Iran and indicates that the vertical range is greater than was previously thought. The related new genus *Derikaspis* occurs elsewhere in France, where *D. brianensis* (Courtessole, 1973) is rare in Niveau H of the Montagne Noire.

An earlier summary of the Sosink Formation's trilobites (Dean 1975 : 364; figs 2, 8) provisionally correlated the formation with the middle half of the Middle Cambrian, an assessment I now consider too low, judging from published correlations of the Scandinavian, Spanish and French successions. Within the shaly lowest 193 m of the Sosink Formation, the

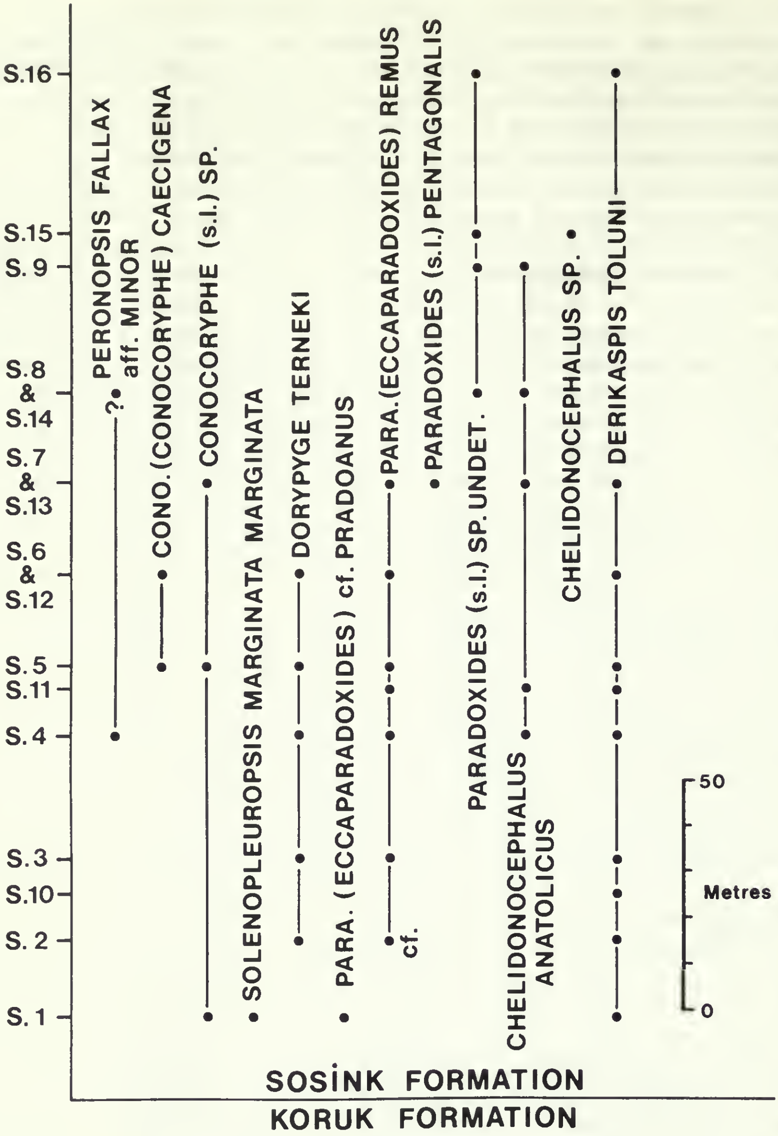

Fig. 68 Distribution of trilobites in lowest part of Sosink Formation. Locality numbers refer to Fig. 1, p. 3.

oldest fossiliferous horizon, S.1, is correlated with the highest strata containing *Solenopleuropsis* in both the Montagne Noire (Niveau F) and northern Spain, and thus with the highest part of the *Paradoxides paradoxissimus* 'Stage' of Sweden. A correlation of higher fossiliferous horizons in the shales with the lower two-thirds of the *Paradoxides forchhammeri* 'Stage' is suggested by the resemblance of *Peronopsis fallax* aff. *minor* and *Dorypyge terneki* to material from the *Solenopleura brachymetopa* Zone, and receives general support from the presence of *Derikaspis* in Niveau H of the Montagne Noire.

Fossils are uncommon and poorly preserved in the highest shales but undetermined fragments of *Paradoxides* (s.l.) at S.15, where they are accompanied by *Chelidonocephalus* sp., are evidence of a Middle Cambrian age. Fossils become still rarer in the overlying 865 m of sandstones, siltstones and silty shales which make up the remaining Sosink Formation as measured by Kellogg (1960). The significance of *Holasaphus mesopotamicus* about 500 m above the base of the formation has already been discussed (Dean 1972); in spite of the absence of paradoxidids, a Middle Cambrian age still appears likely by analogy with *Holasaphus* in eastern Canada and the resemblance of *H. mesopotamicus* to *Andrarina costata* (Angelin) from the *Lejopyge laevigata* Zone of Sweden. There is as yet no evidence as to whether the upper half of the Sosink Formation is also of Middle Cambrian age or extends into the Upper Cambrian. Elsewhere in Turkey the faunas of the lower Sosink Formation may be represented in the Yerlikaş Formation (Ketin 1966 : 80) of the Penbeğli–Tut area, about 240 km west of Derik, where paradoxidids and *Solenopleuropsis* have been reported (Dean 1975 : 364). A record of *Solenopleuropsis* (Dean *in* Dean & Monod 1970 : 418) from the red nodular limestone member, highest unit of the Çal Tepe Formation near Seydişehir, is now known to be incorrect: the specimen in question is a fragment of *Pardailhania* and the whole of the Çal Tepe Formation is older than the Sosink Formation.

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Accepted for publication 5 May 1981

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An account of the Ordovician rocks of the Shelve Inlier in west Salop and part of north Powys

By the late W. F. Whittard, F.R.S. (Compiled by W. T. Dean)

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The Geology Series is edited in the Museum's Department of Palaeontology
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ISSN 0007-1471

British Museum (Natural History)
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British Dinantian (Lower Carboniferous) Terebratulid Brachiopods

C. H. C. Brunton

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Synopsis

Six genera of terebratulid brachiopods are recognized in the British Dinantian rocks; their principal characteristics, especially the dispositions of their hinge plates, are described to allow recognition. The name *Dielasma hastata* (J. de C. Sowerby), of much previous literature, is shown to include several species and the true *hastata* is redescribed within the genus *Beecheria*. The new species *Harttella oakleyi* is described.

Introduction

In Britain, and indeed most of Europe, Carboniferous terebratulids have received little attention taxonomically, and have never been reviewed. This study arose from, and extends beyond, the investigations into four taxa found in the acid-developed silicified faunas of County Fermanagh, Ireland (see Brunton 1966, 1968). These four terebratulids are described in detail elsewhere (in preparation), but investigations of their taxonomic positions made it clear that many more terebratulids are to be found in Britain than one would think from the literature.

Silurian and Devonian terebratulids have been described by Cloud (1942) and Permian taxa by Campbell (1965) and Stehli (1956, 1961, 1965). However, in Britain the literature abounds with references to *Dielasma hastata* (J. de C. Sowerby), but little else. *Alwynia* was described by Stehli (1961), based upon *Terebratula vesicularis* de Koninck, which is recorded from the Isle of Man, and the species *Terebratula sacculus* J. de C. Sowerby has been placed by some authors in *Girtyella* (e.g. Muir-Wood 1951).

Terebratulids present serious difficulties to the taxonomist because many taxa resemble each other externally, whilst having distinctive internal morphologies. Particularly in the Mesozoic this problem has been attacked by serially sectioning specimens in attempts to see or reconstruct their internal morphologies. The sectioning of Lower Carboniferous specimens, plus information from silicified material, allows the easy recognition of six genera of terebratulids. In addition the necessary computing facilities have become available which allow a series of drawings of serial sections to be entered to a computer programmed to provide drawings, or screen display, of the specimen viewed from any direction and as if restored to three dimensions. Stereo-pairs of these drawings allow viewing with a three-dimensional effect (Fig. 20, p. 55). This technique allows accurate drawings of the shell interior to be reproduced easily, whereas in the past complex drafting techniques, or sheer guesswork, were used.

Palaeozoic terebratulids were described by Stehli in the *Treatise* (1965), with the emphasis of classification being upon the length of the loop, which in life supported the lophophore. In the introduction to the Terebratellidina Muir-Wood & Stehli wrote in the *Treatise* (Stehli 1965 : H730): 'For the Terebratulida as a whole, we still lack essential information concerning internal characters, especially of the Triassic genera, and consequently it is not now possible to shape a sound classification or to give a satisfactory outline of evolution.' Dagys accepted this challenge and in 1972 published a reclassification of terebratulids, based

Bull. Br. Mus. nat. Hist. (Geol.) **36** (2): 45–57

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largely upon his experience of Triassic species. Dagys was less concerned with loop length than with the form and ontogeny of the cardinalia as a whole. In particular the development and dispositions of the hinge plates in dorsal valves are important in characterizing genera and suprageneric groups. Of the seven superfamilies Dagys (1972) recognized within the Terebratulida, two are represented in the Carboniferous of Europe by the following genera:

- Cryptonellacea
  - Cryptonellidae
    - *Cryptonella*
  - Cranaenidae
    - *Girtyella*
    - *Harttella*
  - Notothyridae
    - *Alwynia*
- Dielasmatacea
  - Dielasmatidae
    - *Dielasma?*
    - *Balanoconcha*
  - Heterelasminidae
    - *Beecheria*

In these Carboniferous genera, those which in adulthood have entire hinge plates free of the valve floor (other than for connections to a median septum) fall into the Cryptonellacea, while the dielasmatacean genera have hinge plates joining to the valve floor medially and tending to separate anteriorly. Each genus has a distinctive combination of hinge plate dispositions and presence or absence of dental plates (Fig. 1, A–F). Thus a section perpendicular to the long axis of the shell a few mm from the dorsal umbo, and a check on the ventral umbo for dental plates, allows generic assignment. The presence of true *Dielasma* in the British Carboniferous is now in doubt and the genus is not described here.

Specific differences are to be found externally in the shell form and the details of shape of the anterior commissure, internally in details of hinge plate morphology, disposition of the crura and details of the pedicle aperture. When preserved, colour banding is also probably specific, as may be the density of endopuncta within the shell. This last feature has been discussed for fossil terebratulids by Campbell (1965) and for Recent species by Foster (1974). They suggested that ecological conditions dictated endopunctal densities, so that species in

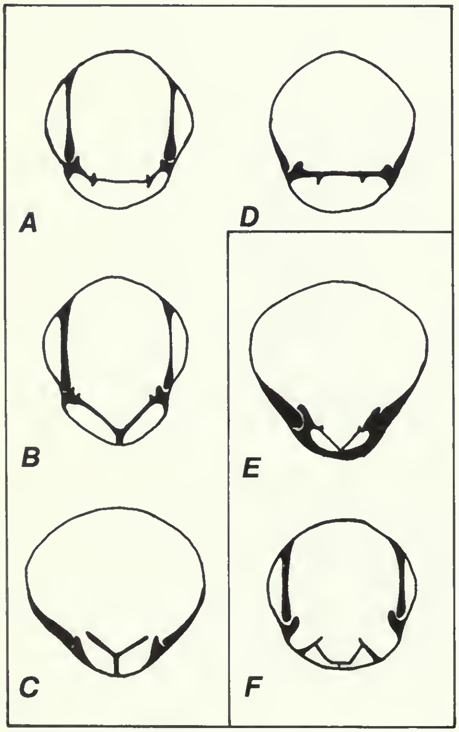


Fig. 1 Transverse sections through the umbonal regions of six Dinantian terebratulid genera. The orientation of the sections is with dorsal valves downwards. Sections A–D, *Cryptonella*, *Girtyella*, *Harttella* and *Alwynia* respectively, belong in the Cryptonellacea, while sections E and F, *Balanoconcha* and *Beecheria*, belong in the Dielasmatacea. The appearance of the dorsal sockets and hinge plates varies according to the positions of the sections. Thus *Harttella* (C) cut nearer the umbo shows hinge plates and socket ridges united in a similar fashion to *Girtyella* (B). *Balanoconcha* (E) cut further from the umbo would show the inner hinge plates separated on the valve floor medially.

warm waters may have more endopunctae per mm² than those in cold water. This, however, cannot be the only answer since four species occurring together in County Fermanagh display a wide variation in endopunctal densities. It seems likely that zoological differences at species level are fundamentally important, but that variations occur intraspecifically which are influenced by ecology. Thus the Fermanagh *Cryptonella* species has high endopunctal densities (at about 450 per mm²) while the other species rate between 100 to 250 per mm².

Systematic palaeontology

In this section each of the six British Carboniferous genera is briefly described and characterized. Under *Beecheria* more information is provided, since this genus is to a large extent replacing the name *Dielasma*.

Synonymy notations are as in Matthews (1973).

Genus *CRYPTONELLA* Hall, 1861

TYPE SPECIES. *Terebratula rectirostra* Hall, 1860, from the mid-Devonian of North America.

REMARKS. The relatively long-looped cryptonellids are seldom recorded from the Carboniferous of Europe and in general *Cryptonella* itself is similar externally to genera like *Cranaena* or *Dielasma*. The loops in terebratulids are commonly broken so *Cryptonella* must be recognized by other means. One characteristic is that the ventral umbo of *Cryptonella* species is nearly straight to suberect in position, and so leaves the deltidial plates exposed (Fig. 2), in contrast to the more strongly incurved beaks of most other genera. In addition the endopunctation of Carboniferous *Cryptonella* is fine and very abundant, there being approximately 450 endopuncta per mm², more than twice the density of other Carboniferous genera. Internally, the disposition of the hinge plates resembles that of *Alwynia*, but the latter has no dental plates. In detail the hinge plate is perforated posteriorly and remains unsupported between the inner socket ridges. The crural bases, which are close to the socket ridges, form ridges on both the dorsal and ventral surfaces of the hinge plate. Dental plates are usually well developed (Fig. 3). *Cryptonella* species in the British Dinantian resemble some *Girtyella* species and, other than by endopunctation, the two groups are best differentiated by their internal morphologies.

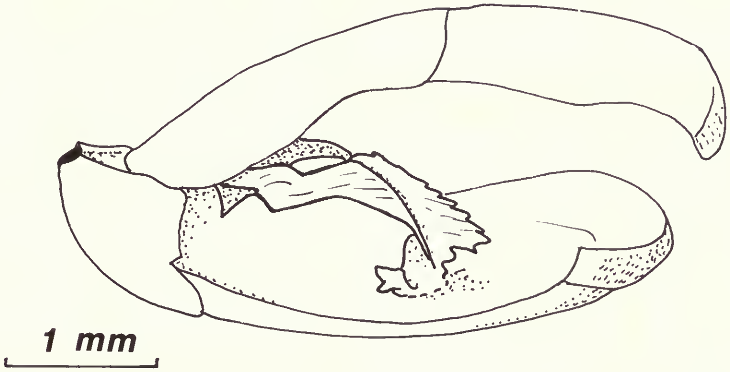


Fig. 2 Drawing of a lateral view of a silicified juvenile specimen of *Cryptonella* sp. from Co. Fermanagh, Ireland, showing the almost straight ventral umbo and immature (cryptacanthiiform) loop, the ventral tip of which, in this specimen, is cemented by siliceous deposits to the ventral valve.

Amongst the many terebratulids described by de Koninck (1887), two externally resemble

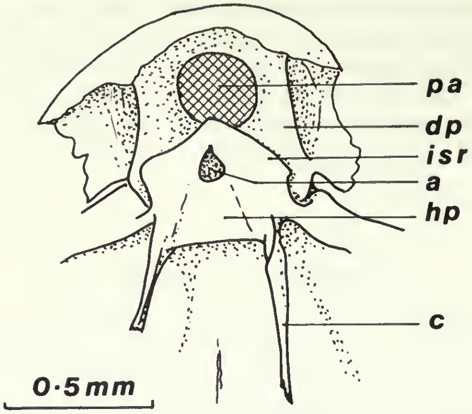


Fig. 3 Drawing of the internal posterior region of a silicified *Cryptonella* sp. from Ireland. The ventral umbo, with its pedicle aperture (pa) and dental plates (dp), is uppermost. The aperture (a) at the posterior end of the hinge plate (hp) leads to the cavity below the hinge plate. Indistinct outer hinge plates connect the inner socket ridges (isr) to the crural bases, from which the crura (c) extend anteriorly.

Cryptonella and may belong here; they are *Dielasma amygdaloides* (1887 : pl. 4, figs 26–40) and *D. subfusiforme* (1887 : pl. 5, figs 32–44).

Cryptonellid genera have been described in detail from the Permian of SW Texas by Cooper & Grant (1976).

Genus *GIRTYELLA* Weller, 1911

Type species. *Hattinia indianensis* Girty, 1908, from the Pella beds of Iowa, correlated with the late Meramec Ste Geneviève limestones, considered to be of late Asbian age.

Remarks. It should be noted that the *Treatise* illustration (Stehli 1965 : fig. 614.2b) of the genus is poor in that the inner hinge plates should be concave onto the low median septum, forming a distinct Y-shaped structure in cross section (Fig. 1B), as originally illustrated by Weller (1911). *Girtyella* resembles the Permian genus *Fletcherithyris* Campbell internally,

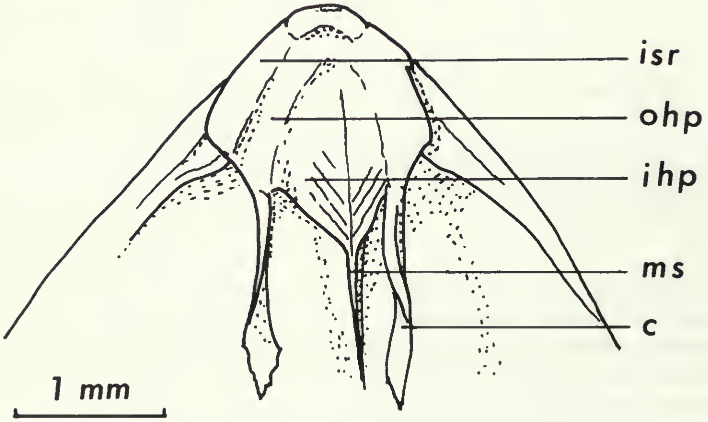


Fig. 4 Drawing of the internal posterior region of a dorsal valve of a silicified *Girtyella* sp. There is a weakly differentiated cardinal process posteriorly. The inner socket ridges (isr) and outer hinge plates (ohp) merge to the crural bases. The inner hinge plates (ihp) are supported on a median septum (ms) which does not appear centrally placed because this is a slightly oblique view. These form a Y-shaped structure when seen in section.

but the former has a persistent median septum while in the Permian genus it only raised the inner hinge plates off the valve floor late in ontogeny. In addition the endopunctal density is very low in *Fletcherithyris*, being less than half the 250 or so per mm^2 expected in *Girtyella*.

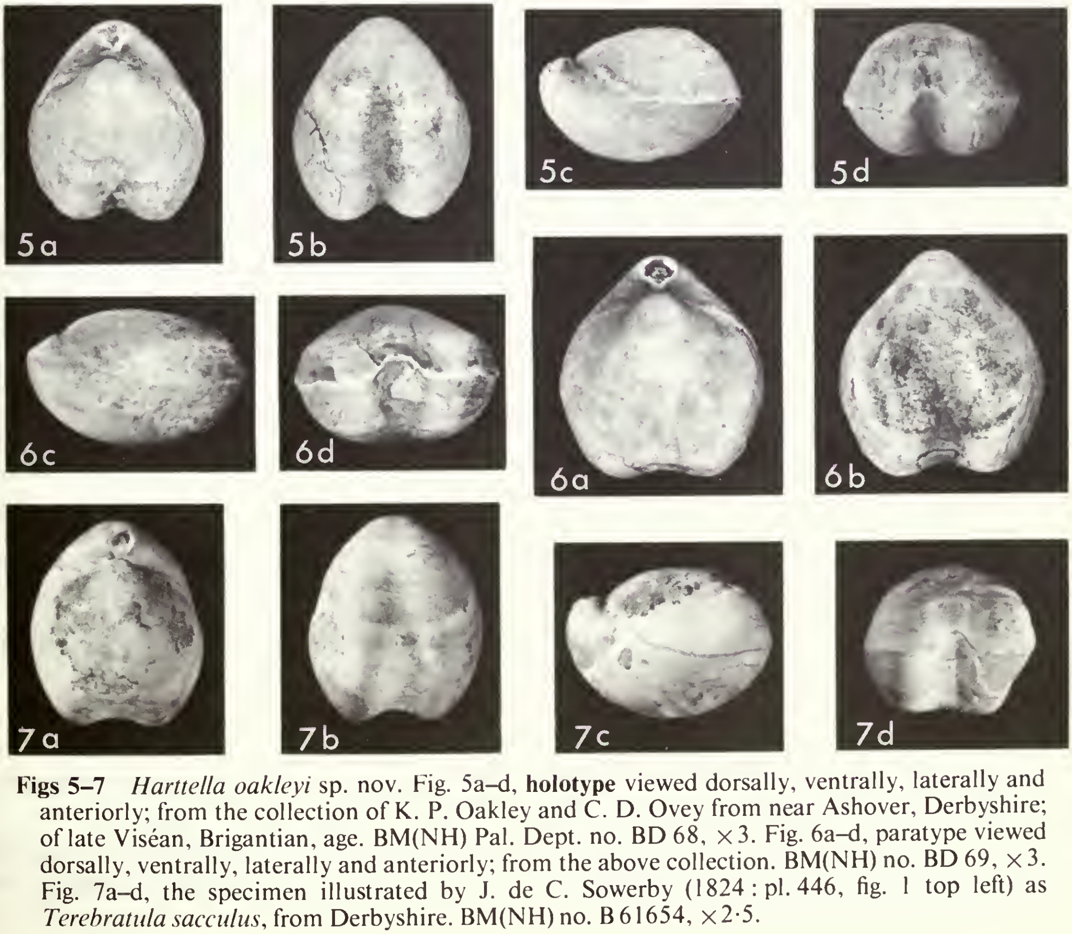
Girtyella species are small to medium-sized, they tend to be fat, i.e. broad and strongly biconvex, and commonly have late stage sulci in their valves. Internally the ventral valve has dental plates, although they may be short, and the hinge plates form a Y-shaped structure by fusion with the persistent median septum. The crural bases are close to the inner socket ridges and can be traced on the ventral surface of the hinge plates (Fig. 4).

Muir-Wood (1951) suggested that *Terebratula sacculus* J. de C. Sowerby belonged to this genus. However, inspection of the lectotype and other specimens leads me to believe that it should be assigned to *Balanoconcha* Campbell (see p. 52).

Genus *HARTTELLA* Bell, 1929

TYPE SPECIES. *H. parva* Bell, 1929, from the Lower Windsor Group (Zone B of Bell), Nova Scotia, Canada. On micropalaeontological evidence Jansa, Mamet & Roux (1978) correlate these beds with late Viséan strata of western Europe.

REMARKS. This genus, not previously recognized in Europe, is small, commonly no more than 10 mm long, either smooth or with a deep ventral valve sulcus, especially anteriorly. Internally the genus lacks dental plates and the hinge plates fuse medially onto a median septum, forming a Y-shaped structure (Fig. 1C), as in *Girtyella*.



Figs 5–7 *Harttella oakleyi* sp. nov. Fig. 5a–d, **holotype** viewed dorsally, ventrally, laterally and anteriorly; from the collection of K. P. Oakley and C. D. Ovey from near Ashover, Derbyshire; of late Viséan, Brigantian, age. BM(NH) Pal. Dept. no. BD 68, ×3. Fig. 6a–d, paratype viewed dorsally, ventrally, laterally and anteriorly; from the above collection. BM(NH) no. BD 69, ×3. Fig. 7a–d, the specimen illustrated by J. de C. Sowerby (1824 : pl. 446, fig. 1 top left) as *Terebratula sacculus*, from Derbyshire. BM(NH) no. B 61654, ×2·5.

In describing *T. sacculus*, J. de C. Sowerby (1824 : pl. 446, fig. 1 top left) illustrated a specimen which is, in fact, a *Harttella* species (Figs 7a–d). Other examples of the genus in the BM(NH) collections include those described below as *H. oakleyi* sp. nov., and about thirty congeneric specimens collected by the author from near Middleton in Teesdale.

The type species, *H. parva*, lacks folding, but another Windsor Group species, *H. gibbosa* Bell, from beds approximately equivalent to the late Viséan of Europe, is sulcate in a similar fashion to the new British species.

Harttella oakleyi sp. nov.
Figs 5–7

v. 1824 *Terebratula sacculus* J. de C. Sowerby: 65; pl. 446, fig. 1 top left.

DIAGNOSIS. *Harttella* with strong, persistant ventral valve sulcus and uniplicate commissural fold.

DESCRIPTION. Small (up to 10 mm long) shells with prominent, erect, ventral umbo. Strongly biconvex lateral profile with opposed growth anteriorly in adulthood. Ventral valve with increasingly deep sulcus developed from about 4 mm from umbo and forming narrow uniplicate fold in anterior commissure and ligate outline. Hinge plates raised on high median septum anteriorly and crural bases springing from their ventral surfaces.

NAME. The type specimens are named after the late Dr Kenneth P. Oakley, of the British Museum (Natural History), who collected them in 1946.

HOLOTYPE. BM(NH) Palaeont. Dept. no. BD 68, collected by K. P. Oakley and C. D. Ovey from Fall Hill quarry, Milltown, near Ashover, Derbyshire, from late Viséan (Brigantian) limestones. Fig. 5a–d.

MATERIAL. Approximately fifty other specimens from the Oakley & Ovey collection, nos BD 69–BD 79. A single specimen in the Sowerby Collection, figured by J. de C. Sowerby (1824), B 61650, and probably collected between Matlock and Derby.

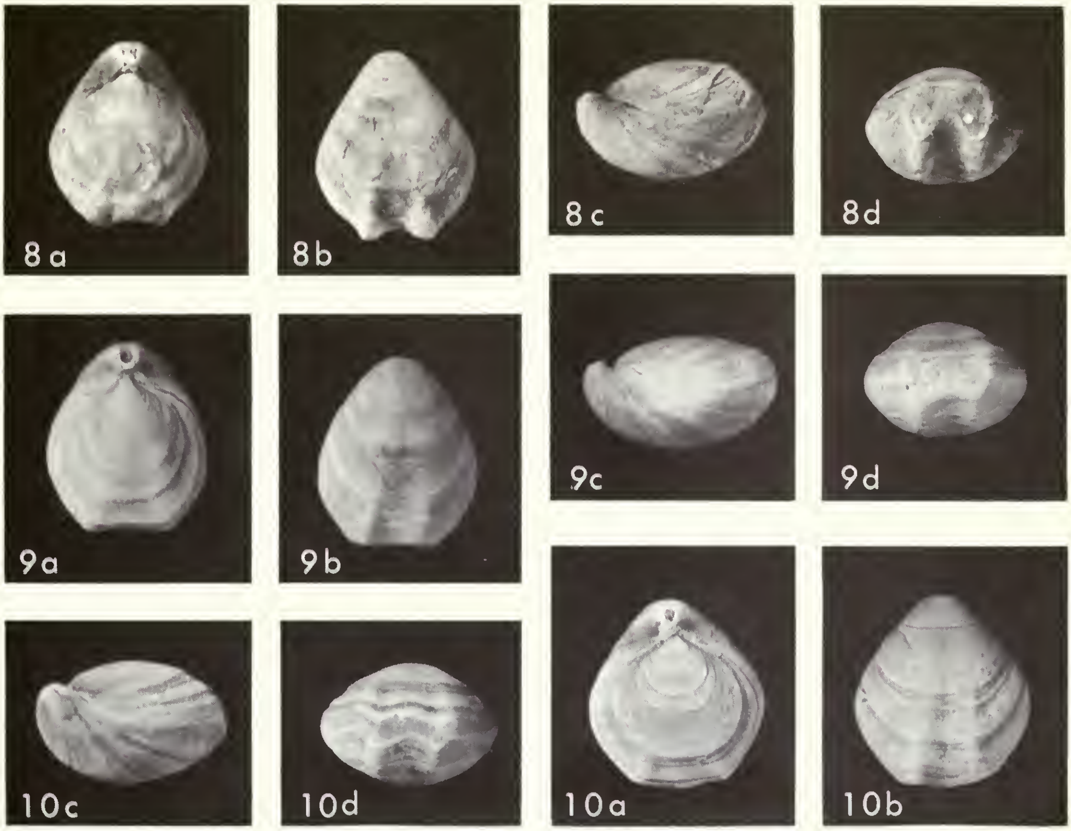
REMARKS. *H. oakleyi* externally somewhat resembles *B. saccula*, to which it has normally been attributed in the past, but differs in being smaller (adults being less than half the length of *B. saccula*) and in having a much more strongly developed sulcus in the ventral valve. In *B. saccula* the ventral sulcus developed late in ontogeny and the dorsal valve commonly remained only slightly affected at the commissure. In contrast the ventral sulcus of *H. oakleyi* started within about 4 mm of the ventral umbo (i.e. at less than half the adult shell length) and persisted, with increasing width and depth, to the ligate anterior margin where the commissure is sharply uniplicate (Figs 5–7, b, d). In some specimens the ligate nature of the anterior margin is accentuated by an anteriorly developed groove on the dorsal valve. Internally, the dispositions of the hinge plates in these two species are quite different (Fig. 1C, E). The species differs from *H. gibbosa* Bell in having a ventral sulcus originating close to the umbo; in Bell's species the sulcus is restricted anteriorly. Judged on Bell's serial sections (1929 : 151), the dorsal valve is more heavily thickened around the sockets than in the British species.

At present *H. oakleyi* is known only from late Viséan limestones in Derbyshire, but closely related specimens are known from the early Namurian of Yorkshire.

Genus *ALWYNIA* Stehli, 1961

TYPE SPECIES. *Terebratula vesicularis* de Koninck, 1851, a rare species from the Visé district of Belgium, probably of mid to late Viséan age.

LECTOTYPE. Here selected, specimen in the de Koninck Collection of the British Museum (Natural History) Palaeont. Dept., no. BD 80, from the Visé region of Belgium. None of the ten de Koninck specimens looks like the original 1851 figuring, but the chosen specimen matches closely to that later figured by de Koninck (1887 : pl. 8, figs 30–33) and is illustrated here (Fig. 8a–d).



Figs 8–10 *Alwynia vesicularis* (de Koninck). Fig. 8a–d, **lectotype** viewed dorsally, ventrally, laterally and anteriorly; from de Koninck's collection from the Visé region of Belgium; of mid to late Viséan age. BM(NH) Pal. Dept. no. BD 80, ×2·5. Fig. 9a–d, a second specimen from de Koninck's collection, viewed dorsally, ventrally, laterally and anteriorly. BM(NH) no. BD 86, ×2. Fig. 10a–d, a third specimen from the same collection, viewed dorsally, ventrally, laterally and anteriorly. BM(NH) no. BD 85, ×2.

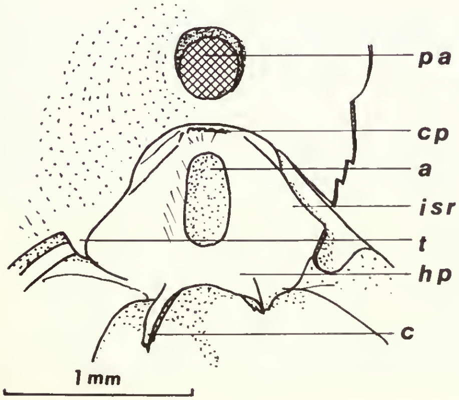


Fig. 11 Drawing of the interior posterior region of a silicified *Alwynia* specimen from Ireland. The ventral valve is uppermost and has a thickened rim to the pedicle aperture (pa). The dorsal valve has a weakly developed cardinal process (cp), a large aperture (a) in the hinge plate (hp) and crural bases forming ridges on the underside (dorsal surface) of the hinge plate. The crus (c) on the right, as well as the anterior end of the socket, is broken.

REMARKS. Stehli (1961) included only the type species in the genus, although a second species is now known from Ireland. These are small, relatively deep-bodied species with anteriorly developed opposite or alternate folding. In *A. vesicularis* this forms a characteristic antiplicate anterior commissure (Fig. 8d), while in the Irish species the commissure is rectimarginate but with a ligate anterior margin. *Alwynia* species resemble *T. sacculus*, but internally the two differ considerably. *Alwynia* has no dental plates and the hinge plates form a horizontal, medially unsupported, structure with the crural bases forming ridges on its dorsal surface (Fig. 11).

Specimens from the type locality, Visé, are likely to be of Asbian age, as are those specimens of *A. vesicularis* known from the Isle of Man. The Irish species is also of Asbian age.

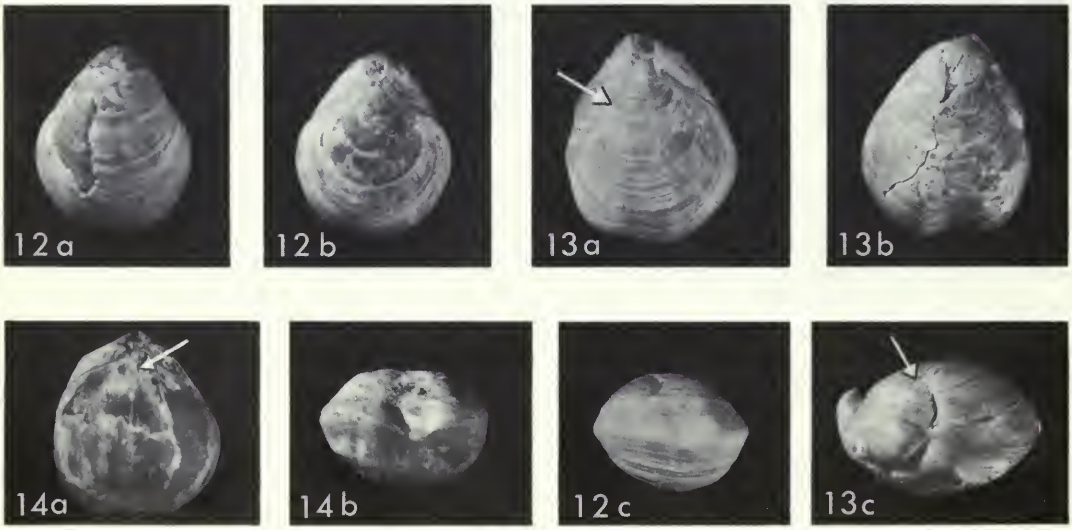
Genus *BALANOCONCHA* Campbell, 1957

TYPE SPECIES. *B. elliptica* Campbell, 1957, from the Watts district of New South Wales, Australia. When first described the age of these beds was thought to be Tournaisian, but recent work has assigned them to a mid to upper Viséan age (Roberts 1975).

REMARKS. This Australian Viséan genus was discovered when trying to assign *T. sacculus* J. de C. Sowerby to a modern genus, having realised that it could not be included in *Girtyella*. *Balanoconcha* is characterized by having no dental plates in the ventral valve and inner hinge plates which fuse to the dorsal valve floor medially forming a V-shaped structure posteriorly (Fig. 1E), but separating anteriorly, as in *Dielasma* (which has dental plates).

When selecting the lectotype of *T. sacculus* (Fig. 14), Muir-Wood (1951) thought the specimen contained a single dental plate. This piece of shell is, I think, not a dental plate but a shelly fragment trapped in the ventral umbo. Several other specimens, matching the type externally, were sectioned and all display the internal structures characteristic of *Balanoconcha*.

Externally *Balanoconcha* resembles *Alwynia* in being somewhat rounded with anterior



Figs 12–14 *Balanoconcha saccula* (J. de C. Sowerby). Fig. 12a–c, ventral, dorsal and anterior (note, ventral valve upper) views of a specimen from Narrowdale, near Alstonfield, Staffordshire. BM(NH) Pal. Dept. no. B 49340, ×1·5. Fig. 13a–c, dorsal, ventral and lateral views of a specimen from the same locality which, when young, was severely damaged (arrowed) and grew asymmetrically with scar tissue on both valves. BM(NH) no. B 49341, ×1·5. Fig. 14a, b, lectotype (sel. Muir-Wood, 1951), viewed dorsally (showing the median septum, arrowed) and anteriorly (ventral valve uppermost), from the Sowerby collection. BM(NH) no. B 61653, ×1·5.

folding. Most of the specimens up to lengths of about 25 mm from Treak Cliff, Derbyshire, described by Parkinson (1952) as *Dielasma hastata* (J. de C. Sowerby), are in fact specimens of *B. saccula*, but the largest specimens in that study belong to *Beecheria*: see below. These seem to be the commonest two species at Treak Cliff and from similar 'reef' environments of Asbian age, where *Dielasma* s.s. species have not, as yet, been recognized. The latter are more typical of Permian rocks.

Genus ***BEECHERIA*** Hall & Clarke, 1894

TYPE SPECIES. *B. davidsoni* Hall & Clarke, 1893, from the Windsor Group of Nova Scotia, Canada.

REMARKS. This genus was first separated from *Dielasma* in the mistaken belief that it had no dental plates. Bell (1929), in his study of Windsor Group faunas, discovered dental plates in the type species and reassigned it to *Dielasma*. Stehli (1956) revived *Beecheria*, recognizing that the dorsal cardinalia, in particular the hinge plates, differed, but he did not use topotypic material and provided illustrations of the internal morphology which do not match that of *B. davidsoni* (see Campbell 1965). Although the lectotype (Chicago University Museum catalogue no. 12223-475) is relatively short at 15·6 mm long, other specimens are bigger and other *Beecheria* species reach over 50 mm in length. They are amongst the largest Carboniferous terebratulids.

Beecheria species have not been recorded commonly from western Europe. However, inspection of our commonly quoted British terebratulid, *Terebratula hastata* J. de C. Sowerby, reveals that it belongs to *Beecheria*, and that other similar species also belong in this genus.

Beecheria is elongate in outline, with a somewhat flattened dorsal valve, when seen in profile. The anterior shell outline is rounded to emarginate, and the commissure is rectimarginate. Internally the ventral umbo has dental plates and in the dorsal valve the inner and outer hinge plates form a pair of V-shaped structures, widening onto the valve floor (Fig. 1F). Thus the inner socket ridges and outer hinge plates separate, and the median edges of the inner hinge plates also separate anteriorly on the valve floor. In this median space there is a delicate shelly platform barely separated from the valve floor (Fig. 15), which in life probably accommodated the ends of muscles.

Beecheria species include *B. hastata* (see below), a new species to be based upon specimens from Ireland and Derbyshire, specimens named as *Dielasma tumidum* by de Koninck (1887) from Belgium, and several species described by Weller (1914) from the Mississippi valley of the U.S.A. These range through much of the Viséan, but they are, perhaps, commonest in early to mid-Viséan strata.

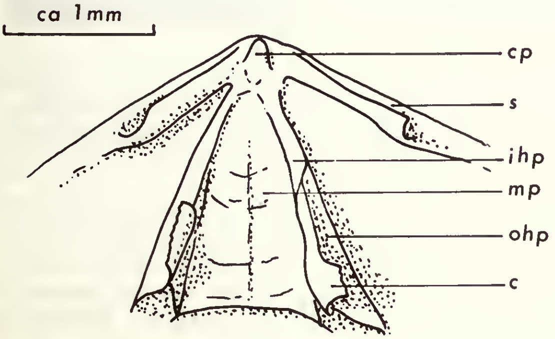


Fig. 15 Drawing of the posterior region of the dorsal valve interior of a silicified specimen of *Beecheria* from Ireland. Adult specimens have a weakly differentiated cardinal process (cp). The sockets (s) are widely separated from the outer and inner hinge plates (ohp, ihp) which form inverted V-shaped structures on the valve floor, well seen in sections (see Fig. 1F). The crural bases extend from the outer hinge plates as increasingly high ridges until, anteriorly, the crura (c) curve away ventrally. Medially, between the inner hinge plates, there is a slightly raised median platform (mp) of shell supported by a median ridge.

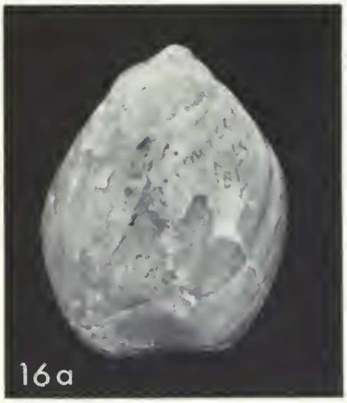
Beecheria hastata (J. de C. Sowerby, 1824)
Figs 16, 17

v* 1824 *Terebratula hastata* J. de C. Sowerby: 66; pl. 446, figs 2, 3.
p. 1858 *T. hastata* Sowerby; Davidson: 11; pl. 1, figs 1–3. 12.

Diagnosis. Large (reaching 40 to 50 mm long) ovate *Beecheria* with straight to emarginate anterior margin, commissure rectimarginate. Ventral valve with shallow, flat-floored sulcus from about 25 mm length to anterior; there may be a slight dorsal valve anterior sulcation.

Type specimen. *Terebratula hastata*, BM(NH) Palaeont. Dept. no. B 61657, figured by Sowerby (1824) in the centre of his pl. 446; presented to him by Mr S. Wright. Parkinson (1952), informally by inference, selected this specimen as lectotype (Fig. 16a–c).

Locality and horizon. Sowerby's locality is Limerick, Ireland, the exact locality being unknown. Douglas (1909), writing of *Dielasma hastata* from County Clare, said 'Sowerby's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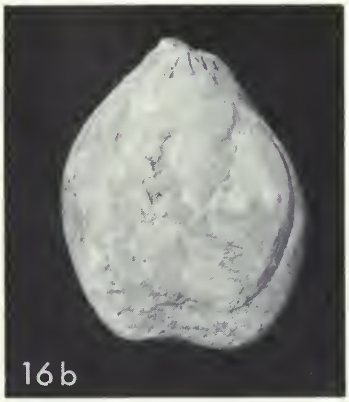
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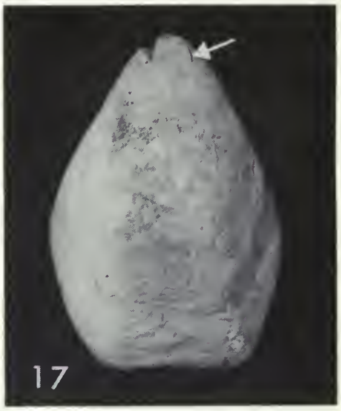
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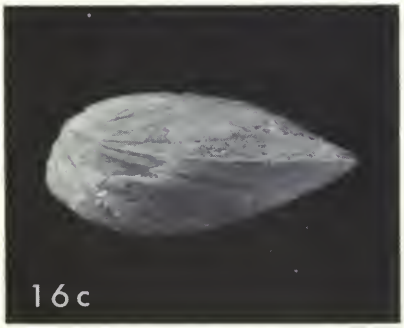
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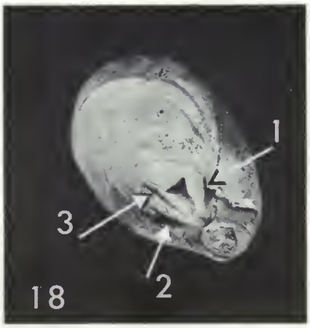

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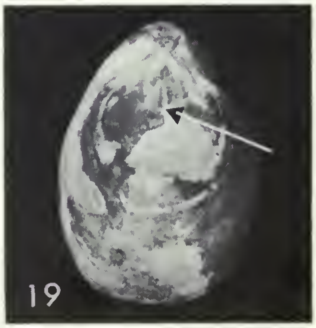
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Figs 16, 17 *Beecheria hastata* (J. de C. Sowerby). Fig. 16a–c, lectotype (sel. Parkinson, 1952), viewed ventrally, dorsally and laterally; from the Sowerby collection, Limerick, Ireland; of early Viséan age. BM(NH) Pal. Dept. no. B 61657, × 1. Fig. 17, ventral view of a specimen, also from Limerick, showing the positions of the dental plates (arrowed); this was sectioned serially to produce Fig. 20. BM(NH) no. B 81014, × 1.

Figs 18, 19 *Beecheria* sp. from Treak Cliff, Castleton, Derbyshire; of late Viséan, Asbian age. Fig. 18, dorsoposterior view of an internal mould showing the positions of dental plates, inner socket ridges (arrow 1), the V-shaped hinge plates (arrow 2) and the median ridge (arrow 3) supporting the median platform. BM(NH) no. BD 3, × 1·5. Fig. 19, a specimen with some of its shell missing showing the appearance of the divergent inner hinge plates and the median platform. BM(NH) no. BD 1, × 1·5.

original type specimen . . . without doubt came from the *Syringothyris* Zone', i.e. that it is of early Viséan age.

REMARKS. The name *hastata* has been a 'sack' name for Carboniferous terebratulids for many decades, and for almost as long it has been assigned to *Dielasma* King, 1859. However, inspection of Sowerby's type specimen (B 61657), which has lost shell from the posteromedian region of the dorsal valve, shows quite clearly that the hinge plates do not fuse with the valve floor as expected in *Dielasma*, but do so along four anteriorly diverging lines (Fig. 16b), as in the genus *Beecheria.* A specimen of *B. hastata* (B 81014, Fig. 17) from Limerick, externally very like the lectotype, has been sectioned serially, giving 66 sections in all. A selection of these sections have been digitized and, by means of a computer, plotted to produce accurate drawings of the internal structures (Fig. 20). These clearly demonstrate the true *Beecheria* character of the cardinalia, including the thin elevated shelly material between the inner hinge plates, recorded also in the type species, *B. davidsoni* (see Fig. 18).

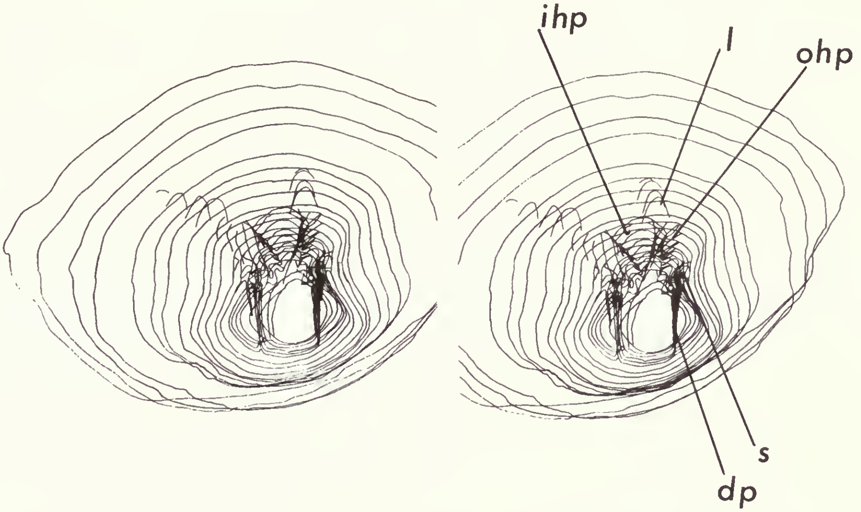

Fig. 20 *Beecheria hastata* (J. de C. Sowerby). Stereoscopic pair of drawings produced from a selection of 19 serial sections (from a total of 66) made from specimen B 81014 (Fig. 17). Each section was digitized and entered to a computer which controlled the plotting of the drawings, arranging them at the correct spacing and at the desired orientations. Use of a pocket stereoscope, with interocular distance of 60–65 mm, should provide full three-dimensional viewing. The posteriormost section was cut at 1·5 mm from the ventral umbo and the anteriormost, nearest, section at 24 mm from the umbo, beyond which point the loop was broken. The ventral valve is to the bottom, with clearly visible dental plates. Viewed posteriorly, into the umbo, tipped dorsally 20° and rotated 13° and 17° from the Z axis on the left and right drawings respectively, to produce an oblique view. ihp = inner hinge plate, l = posterior part of brachial loop, ohp = outer hinge plate, s = socket and dp = dental plate.

In the past the presence of dental plates in a Carboniferous terebratulid has commonly been sufficient evidence for calling it *Dielasma hastata.* Parkinson (1952), in his biometrical study of specimens misidentified as *D. hastata*, wrote of having specimens with dental plates 'sometimes preserved'. In fact his Treak Cliff, Derbyshire sample contained two common species, neither of which is *D. hastata*, pooled to give the presented results. The smaller, fatter individuals reaching about 22 mm long (commonly 16–18 mm long) are *Balanoconcha saccula*, while the thinner specimens with dental plates, reaching about 45 mm long, belong to a *Beecheria* species occurring also in County Fermanagh. This mixture of measurements from two species, one reaching about twice the length of the other, helps to account for the distinct break in slope of 'growth constants' which, as Parkinson (1960) later commented, manifested itself 'by a sudden increase in growth of the length and a temporary cessation of growth in the thickness of the shell'. Below the break specimens are a mixture of the two species, but mostly *B. saccula*; above the break all specimens belong to *Beecheria*.

Conclusions

The genus *Dielasma* King, 1859, is based on the Permian species *D. elongatus* (von Schlotheim). Other well-authenticated species of *Dielasma*, based on internal morphology, are also largely restricted to the Permian. Species of British terebratulids previously attributed to *Dielasma* prove, on studying their interiors, to belong to several genera, in particular to *Beecheria* and *Cryptonella*. Other species, usually of smaller sizes and with sulcate valves, belong to *Balanoconcha*, *Girtyella*, *Alwynia* and *Harttella*. Of these six genera only *Alwynia* had previously been recorded from Britain with certainty. Other than the eastern Australian *Balanoconcha*, the remaining four genera were all described from North American faunas. Despite this wide geographical spread, the ages of species in these genera are broadly comparable, with the exception that *Cryptonella* is recorded throughout the Upper Palaeozoic.

The importance of internal morphology in determining these terebratulids is stressed and these morphologies are believed to be expressed more meaningfully in the classification of Dagys (1972) than in that by Stehli (1965) in the *Treatise*. The presence of hinge plates, which accommodated pedicle adjustor muscles, and the natures of the pedicle apertures in these genera indicate the presence in life of inert pedicles (Richardson 1981) which kept the shell off the substrate but allowed its movement around the pedicle. In Recent terebratulids such pedicles are commonly divided into 'rootlets' at the distal end, allowing attachment to a wide variety of substrates, and the movement around the pedicle allows reorientation in varying water currents to achieve the most advantageous flow through the brachial cavity.

The diversity of six British Dinantian genera, so far recognized, contrasts with twelve Recent genera around the British Isles or seventeen from the Caribbean seas.

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New Microfossil Records in Time and Space

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Synopsis

A Jurassic species of the hitherto Palaeozoic Microproblematicum genus *Aphralysia* is described as *A. jurassica* sp. nov. *Lithothrix* (Algae: Corallinaceae), known from one living species on the North American Pacific coast, now has a fossil record in *L. antiquum* sp. nov. from the late Pleistocene of Mauritius (Indian Ocean).

I. A Jurassic *Aphralysia*

Aphralysia is a somewhat problematic fossil, described by Garwood (1914) as an alga and usually listed as one subsequently. However, Belka (1981) claims it convincingly as a foraminifer. It is a crusting or nodule-forming organism, which in typical vertical cross-section shows a 'fish-scale' or 'blister' pattern of successive irregular layers of thin, calcareous-walled cells which are mostly segment-shaped, i.e. each having a conspicuous outwardly-convex wall and resting below on earlier cells. Other cross-sections, showing irregular vermicular structures, are interpreted by Belka as the horizontal section.

Several species of the genus have been described from the Carboniferous. It is therefore of interest to record the occurrence of a Jurassic example.

MICROPROBLEMATICA

Genus ***APHRALYSIA*** Garwood, 1914, emend. Mamet & Roux 1975, Belka 1981.

TYPE SPECIES. *A. carbonaria* Garwood 1914.

Aphralysia jurassica sp. nov.

Figs 4–6

DESCRIPTION. Crusting *Aphralysia* in which the irregularly-layered cells typical of the main part of the growth show in vertical section as arc-shaped outer walls of dark calcite about 0·005 mm thick. The transverse cell-diameters are about 0·070 mm (up to 0·090 mm) and cell-heights vary according to the convexity and arrangement of the cells beneath, but are always less than the diameters. There is a general irregularity and very occasionally an elongate cell-section is present. A section showing a well-developed growth of smaller vermicular cells, irregularly to tortuously arranged, of which only the very occasional example shows the size and form of the more typical cells, may be a near-horizontal cut.

In the type material the cells show a light brown coloured calcite infill, and the growth encrusts a bivalve shell.

HOLOTYPE. British Museum (Natural History), Dept Palaeontology, register number V.60941. From the Middle Jurassic (Bathonian), Great Oolite, White Limestone, of Quenington Hill, Quenington, Cirencester, Gloucestershire. Figs 4–6.

COMPARISONS. If *A. jurassica* is compared with the other species of the genus (all Carboniferous, except for a qualified Silurian record by Héroux *et al.* 1977), its structures are very much smaller than those of *A. carbonaria* (Garwood 1914, Mamet & Roux 1978)

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and *A. garwoodi* (Hallett 1970). Of the three species described by Mamet & Roux (1975), *A. matthewsi* shows much smaller structures than *A. jurassica* and different cell-form. *A. ferreoli* shows elongate cells in the main layer and a near absence of the distinctively segment-shaped cells typical of the genus. *A. jurassica* seems most similar to *A. capriorae*; the Jurassic material is very limited for an exact comparison of these variable growths.

REMARKS. *Aphralysia* has usually been listed as an alga: Belka claims it as a foraminifer. Like all such crusting organisms, animal or plant, it varies considerably, and named species have necessarily to be defined morphologically on typical structure as preserved, even if they may originally have been ecophenes. For this reason it seems best to describe the Jurassic fossil as new. Whilst perhaps it is not surprising that such a lowly form of Palaeozoic life should persist into mid-Mesozoic, it is surprising that apparently it has not been found before.

STRATIGRAPHIC HORIZON. Quenington Hill and the adjacent Fowler's Hill (SP 1445 0455) are two named roads traversing the same limestone hill: both have only been exposed geologically in the last decade by very rapid 'dig-and-fill' trenching for drainage, etc. Each showed a succession of White Limestone beds capped by Kemble Beds facies. An algal limestone on Fowler's Hill yielded *Dobunniella coriniensis* Elliott, *Pycnoporidium lobatum* Yabe & Toyama, *Ortonella* sp. and cf. *Girvanella* sp., apparently representing the algal horizon described by Elliott (1975) in the upper part of the White Limestone at Daglingworth, Glos. The Quenington Hill *Aphralysia* (with *Pycnoporidium* sp.) occurs at a slightly lower level than this; the only alga from the higher level on Quenington Hill was the well-known *Solenopora jurassica* Brown (also found at Daglingworth).

II. A fossil *Lithothrix*

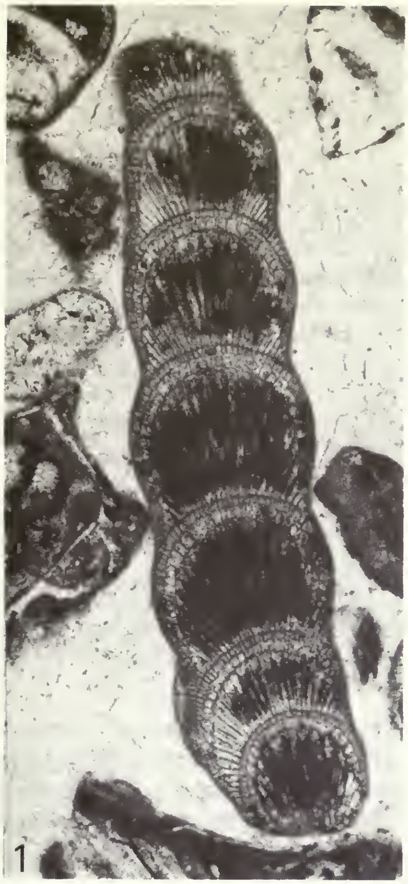
Lithothrix is an uncommon and very distinctive little articulated coralline, known from one living species *L. aspergillum* Gray from the Pacific coast of North America.

It differs in thin-section from all other similar corallines by the arrangement of the cells within the units, most of the medullary area being occupied by one layer only of markedly elongate, thick-walled, dark-staining longitudinal cells. These medullary layers are largely independent in growth of the small peripheral cells, which gave rise to side-branches and to conceptacles. The unusual structure and the growth occasioning it have caused considerable confusion in interpretation (Ganesan & Desikachary 1970, Cabioch 1972, Johansen 1974).

Whatever the detailed anatomical validity of these interpretations, the thin-section appearance of *Lithothrix* is unmistakable. It is therefore of great interest to record a fossil species, which comes from the late-Pleistocene raised reefs of Mauritius in the Indian Ocean. This shows the characteristic cell-morphology of the genus, but differs in external proportions from *L. aspergillum*. Living *Lithothrix* is only known on the Californian–Vancouver coast of North America, and this remarkable occurrence is all we know of its past distribution.

Figs 1–3 *Lithothrix antiquum* sp. nov. Late Pleistocene raised reef; Mauritius, Indian Ocean. All from British Museum (Natural History), Dept Palaeontology, register number V.60116. Fig. 1, **holotype**; longitudinal section, portion of branch, × 70. Fig. 2, random section showing conceptacle (top left), ×78. Fig. 3, transverse section, ×150.

Figs 4–6 *Aphralysia jurassica* sp. nov., **holotype.** Middle Jurassic (Bathonian), Great Oolite, White Limestone; Quenington Hill, Quenington, Gloucestershire, England. All ×90; British Museum (Natural History), Dept Palaeontology, register number V.60941. Fig. 4, portion of encrusting growth showing normal cell-development; vertical section. Fig. 5, portion showing layer of vermicular cells (? horizontal section). Fig. 6, another portion of normal cell-development.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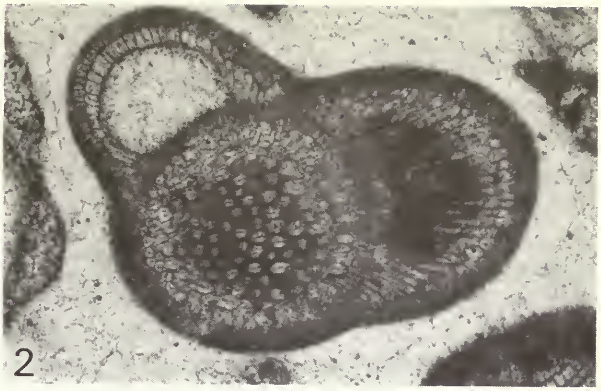
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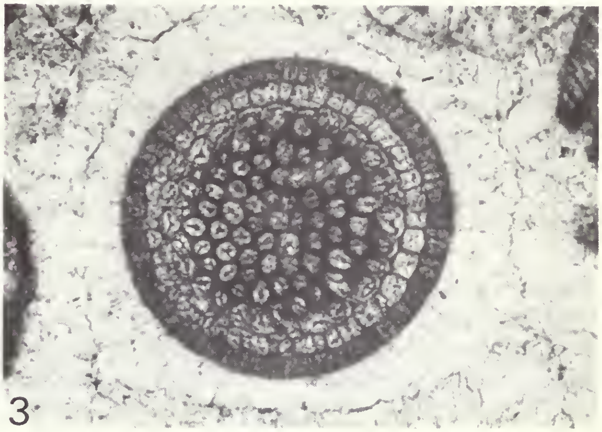
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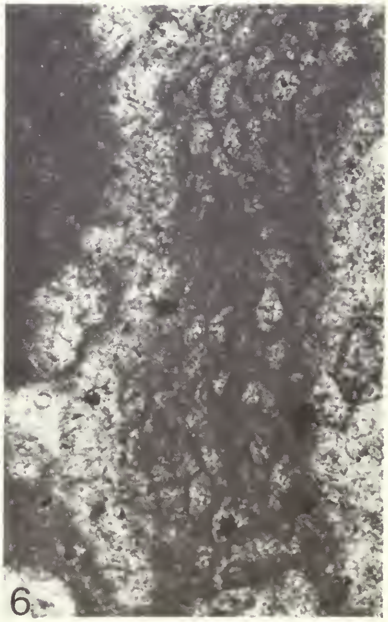
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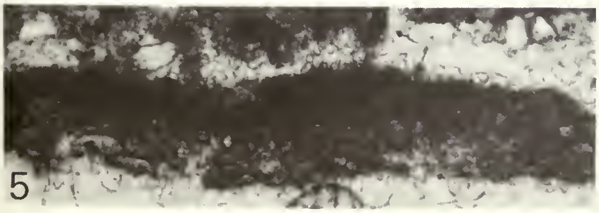
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Alga CORALLINACEAE

Genus *LITHOTHRIX* Gray, 1867

Lithothrix antiquum sp. nov.

Figs 1–3

Diagnosis. *Lithothrix* species in which the 'units' or 'segments' of the calcified branches are wider than high.

Description. Represented fossil by debris, including pieces showing successions of six, seven or eight units; also a presumed lateral conceptacle. Most units are from 0·27–0·36 mm wide: the height is usually a little less than this, occasionally equal. In the living *L. aspergillum* the units are normally consistently elongate, i.e. the height exceeds the width.

The central (medullary) elongate cells are thick-walled and in a conspicuous dark preservation, as in the living species when stained. The peripheral layers of small squarish or rectangular cells are thinner-walled, again as in the living species. A single example of a lateral structure (Fig. 2) is biologically 'empty' (calcite-filled), and is interpreted as probably a former asexual conceptacle. No aperture is seen but the plane of section could have missed it; this infilling is usual in many fossil conceptacles generally. The position relative to the vegetative branch is like that of the living species.

Holotype. British Museum (Natural History), Dept Palaeontology, register number V.60116. From the late Pleistocene raised reefs of Mauritius (Indian Ocean). Fig. 1.

Paratypes. The specimens shown in Figs 2–3, from the same locality and horizon. Reg. no. V.60116.

Remarks. It is regretted that no details of the exact site on Mauritius where the original sample was collected have been preserved. The thin section shows an assemblage of small foraminifera, *Lithothrix*-pieces, and debris of other algae and invertebrates, all set in clear calcite. The genus should logically be represented elsewhere in the Indo-Pacific between Mauritius and North America, but is not known thus to me.

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The Ordovician trilobite *Neseuretus* from Saudi Arabia, and the palaeogeography of the *Neseuretus* fauna related to Gondwanaland in the earlier Ordovician

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Synopsis

Neseuretus tristani (Desmarest) is figured from the Hanadir Shale, Saudi Arabia, only the second Ordovician trilobite described from the Arabian Peninsula. *Neseuretus* was an inshore genus, often accompanied by a sparse fauna of inarticulate brachiopods and bivalves, and confined to the cold-water, and presumably circumpolar shelf seas of the earlier Ordovician. It is regarded as the most sensitive indicator of the former extent of inshore facies in cooler seas fringing Gondwanaland in the earlier (Arenig–Llanvirn) Ordovician. A review of other occurrences of *Neseuretus* supports a united Gondwanaland as deduced from geophysical and whole-fauna evidence, but would also include the southern part of Europe and the southern part of China within the same continental block.

Introduction

As part of the Saudi Arabian Cover Rock Project, staff at the Royal School of Mines (Imperial College) have been mapping the Lower Palaeozoic rocks that outcrop along the edge of the Precambian shield in the mid-part of the Arabian Peninsula. Several highly fossiliferous blocks were recovered from hard bands in the Hanaḍir Shale (Fig. 1), a unit at the base of the Tabuk Formation (Powers *et al.* 1966 : 112; McClure 1978), and overlying the widespread Saq Sandstone Formation of presumed Cambrian to Arenig age. The blocks proved to be crowded with the fragmentary remains of a species of the trilobite *Neseuretus*, accompanied by a few inarticulate brachiopods, bivalves, graptolites, nautiloids and conodonts. The trilobites are well preserved, and since the only other Ordovician trilobite from the Arabian peninsula is a *Plaesiacomia* species described by Thomas (1977), are well worth illustrating. Moreover, *Neseuretus* is a genus of particular palaeobiogeographic significance, and this opportunity is taken to assess its distribution in relation to the Gondwanaland of the earlier Ordovician. We are particularly grateful to Dr J. Ferguson and Dr R. G. Davies for donating this material to us for study. We also thank Dr N. J. Morris and Dr L. R. M. Cocks for determinations.

Palaeogeography of the *Neseuretus* fauna

Definition of the early Ordovician Gondwanaland

Faunas with *Neseuretus* are associated with inshore, epicratonic deposits at what were high latitudes in the earlier part of the Ordovician. Often, as in Saudi Arabia, *Neseuretus* is the only trilobite. Numerous *Neseuretus* may be accompanied by one or two other trilobites such as *Ogyginus*, *Crozonaspis* or *Merlinia*, but apart from a few species of inarticulate brachiopods and bivalves other associated fauna is sparse. Such a low-diversity fauna is

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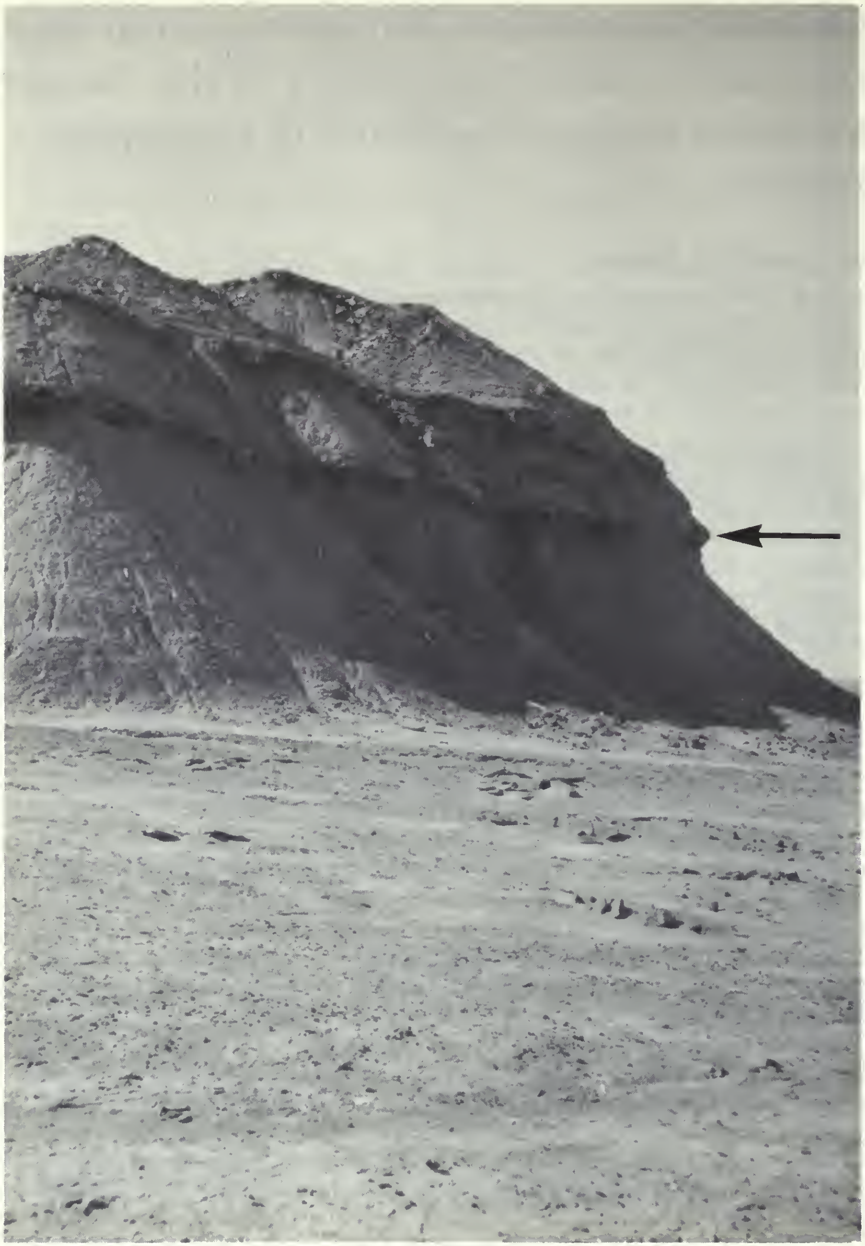


Fig. 1 Photograph of fossiliferous locality at Aţ-Ţīnīyāt, Jabal Shammar, north Saudi Arabia. The arrow indicates the *Neseuretus* horizon. (Photo by Dr J. Ferguson).

exactly what might be expected of an inshore environment at high latitude; the living crab *Hyas coarctatus* is the only well-skeletized decapod species which is at all common at Arctic latitudes today. We regard the *Neseuretus* fauna, and by extension *Neseuretus* itself, as the best indicator of epicontinental seas at relatively high latitudes. Dean (1976) and Cocks & Fortey (1982) used this criterion to infer geographic continuity of the Anglo-Welsh area with southern Europe and north Africa in the earlier Ordovician. We here attempt to extend worldwide the analysis of Dean (1976), to see how the description of this fauna relates to alternative reconstructions of Gondwanaland.

This is a somewhat different approach to deducing continental configuration from that of Whittington & Hughes (1972). These authors compared whole faunas at generic level, and excluded faunas of small diversity ('less than ten taxa'; 1972 : 238). But an important feature of the *Neseuretus* fauna in many occurrences is precisely its low diversity. Here we plot the distribution of a particular facies fauna, the one which, being the most inshore, we deduce would have been most responsive to constraints such as geography and ambient temperature. Deep water faunas include more widespread genera and have more interprovincial 'mixing', albeit with a concomitantly higher diversity. So we contend that the distribution of *Neseuretus* is, *prima facie*, an indication of the extent of relatively high-latitude areas in the Ordovician, and likely also to indicate close geographic proximity. It is important to emphasize that the distribution considerations only apply to the earlier half of the Ordovician, i.e. Arenig to Llandeilo, because many different lines of evidence lead to the conclusion that by the Caradoc palaeogeography and continental distribution were changing fundamentally. We also exclude the distribution of the related genus *Vietnamia* Kobayashi, 1960, but include the subgenus *Neseuretus* (*Neseuretinus*) Dean, 1967, partly because it is difficult to decide to which subgenus poorly preserved species belong.

The distribution of the trilobite *Neseuretus* is paralleled by the distribution of particular suites of sedimentary facies which extend into areas where the characteristic trilobite has not yet been found (Dean 1976). *Neseuretus*-bearing beds are often underlain by and sometimes interbedded with coarse to fine quarzites of Grès Armoricain type. As Bergström (1976) has noted, presumed trilobite trace fossils of the genera *Rusophycus* and *Cruziana* (especially *C. furcifera*) often accompany the *Neseuretus* body fossils. *Neseuretus*-bearing beds are often enriched in iron compounds, as in eastern Newfoundland, parts of southern Europe and in Saudi Arabia. Free calcium carbonate appears to be invariably absent.

Neseuretus has been described from Arenig rocks of the Avalon platform, eastern Newfoundland (Dean & Martin 1978), where it is associated with *Ogyginus* and numerous *Cruziana* trails, and with rich sedimentary ironstones. Arenig occurrences are typical of the transgressive beds at the base of the series in south Wales (Fortey & Owens 1978), and throughout the relatively inshore facies of the Mytton Flags, Shropshire. In the Gorran Quarzites of Cornwall (Sadler 1974) its occurrence is Llandeilian, and Llanvirn-Llandeilo occurrences are typical of a great number of localities in Brittany (Henry 1970) and the Iberian Peninsula (Hammann 1976; Sadler 1974: text-fig. 2), where, however, it is absent from the extreme inshore facies of the underlying Arenig. Destombes (1971) records *Neseuretus* from both Arenig and Llanvirn Formations in Morocco. Dean (1966) has described two *Neseuretus* species from the Montagne Noire, southern France, of Arenig age. Moving eastwards, *Neseuretus* is known from the Arenig of the Taurus Mountains, Turkey (Dean 1971). In Algeria the facies is closely similar to that of Europe (Legrand 1974), inshore and ferruginous with trace fossils and a sparse bivalve and inarticulate brachiopod fauna including *Lingulobolus brimonti*, a species of wide distribution in the Armorican Quartzite facies (see Havlíček, 1980). Whiteman (1971) records *Neseuretus* from a number of Algerian localities, and indicates the continuation of the same suite of rocks into Tunisia. The same facies also continues eastwards into Libya, but we cannot find any faunal records.

The Saudi Arabian occurrence reported here forms a link between the European and African occurrences and those further to the east. There is no published record of *Neseuretus* from Iran and Iraq, although reports of *Cruziana*-rich arenaceous facies (Čtyroky 1973, Dietrich 1937) indicate that the right type of shallow water facies was present in both countries. We accept Dean's (1967) redetermination of *Calymene birmanica* Reed, 1906, from the Shan States, Burma, as a *Neseuretus* species and examination of the types of *Calymene nivalis* Salter (1865*b* : 10) from the Himalayas suggests that this species also may be referred here. In China eight or more species of *Neseuretus* have been reported (from west to east) from the western Yunnan (Sheng 1974), southern Szechwan and southern Shensi (Lu 1975), all from the Llanvirn. The Ordovician faunas in general along this region are of 'European' aspect, and strikingly different from those of north China (e.g. Wang 1980), which are of North American Midcontinent type, and presumably lay near the Ordovician equator, separated by the Tsin Ling suture of Ziegler *et al.* (1977).

In South America *Neseuretus* is recorded from the Llanvirnian of Bolivia (Přibyl & Vaněk 1980), northern Argentina (Harrington & Leanza 1957) and the 'Arenig or Llanvirn' of Peru (Dean 1976 : 243). The 'European' flavour of Ordovician faunas of the northern part of South America has been appreciated for a long time (e.g. Kobayashi 1937), and has recently been emphasized again (Hughes *et al.* 1980) in the case of an offshore fauna from Peru. Whittington & Hughes (1974) emphasize faunal continuity between South America and the rest of Gondwanaland during the Tremadoc. The *Neseuretus* fauna is of limited geographical extent, reflecting the restricted distribution of the appropriate facies in the right climatic zone.

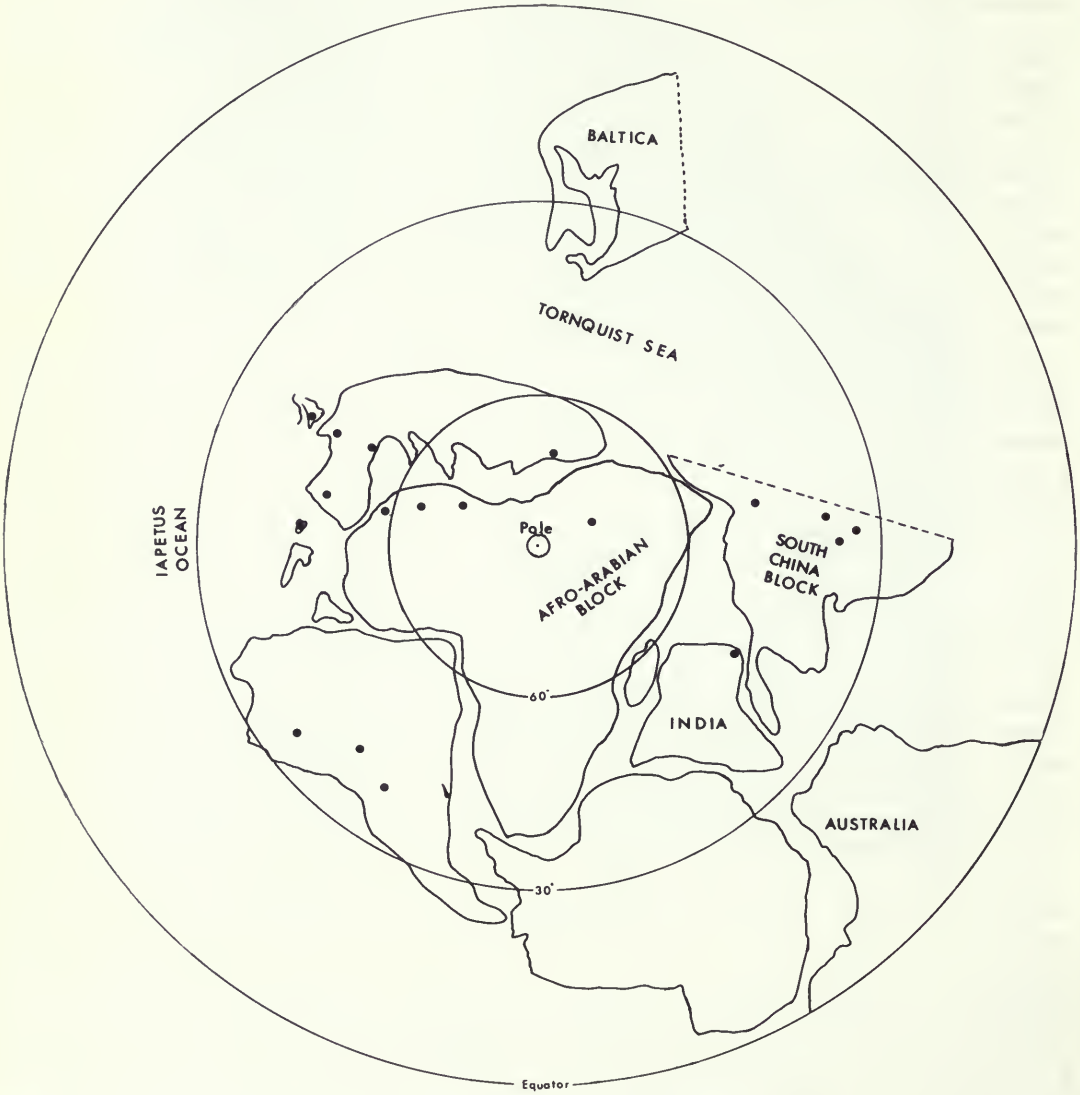


Fig. 2 Palaeogeographic reconstruction of the southern hemisphere (excluding North America) for the Lower Ordovician. The occurrence of *Neseuretus* is indicated. (After Whittington & Hughes 1972).

Gondwanaland in the earlier Ordovician

If the controls on the distribution of *Neseuretus* are as we have suggested it should be a sensitive indicator of the inshore, cold seas of Gondwanaland. This would imply (Fig. 2) a broadly united Gondwanan continent in the earlier Ordovician, including southern Europe attached to north Africa, and including also the southern part of China. This picture is in general agreement with previous Ordovician reconstructions, with Gondwanaland in a polar position (Whittington & Hughes 1972, 1974; Embleton & Valencio 1977; Scotese *et al.* 1979; Bambach, Scotese & Zeigler 1980; Burrett & Richardson 1980). If one makes the assumption that the *Neseuretus* faunas are approximately symmetrically distributed about the pole, this would give a pole position in the region of the eastern part of Africa; the Saudi Arabian occurrence would be closest to the pole. There are, however, several differences between the reconstruction Gondwanaland and adjacent continents based on the distribution of the *Neseuretus* fauna and those cited above.

Scotese *et al.* (1979) and Bambach, Scotese & Zeigler (1980) show the Baltic continent ('Baltica') at very high latitudes in the Middle Ordovician, close to Gondwanaland. This is highly improbable, because the *Neseuretus* fauna is absent from Baltica, and if it was close and at the same latitude there would be no reason to prevent establishment of the fauna. Cocks & Fortey (1982) have advanced reasons why Baltica should be at temperate latitudes and separated from southern Europe by a substantial ocean ('Tornquist's').

Whittington & Hughes (1972: fig. 3) show southern Europe separated from north Africa by a 'Proto-Tethys' ocean. In accordance with Dean (1976), we believe that the distribution of the *Neseuretus* fauna and facies—which extends even to identity at specific level in the Llanvirn—argues against any such oceanic tract. Note that the distribution of the *Neseuretus* fauna is equivalent to the *Selenopeltis* fauna of Whittington & Hughes plus part of the *Asaphopsis* fauna, plus several of those classified as of 'uncertain affinity'. Whittington & Hughes' (1974) Tremadoc faunas are geographically much more widespread, which we would attribute to the transgressive (and hence relatively deep-water and more cosmopolitan) sedimentary regimes on a world-wide scale during this period.

The distribution given here would have to include south-east Asia (including the southern part of China) in Gondwanaland, which differs from the reconstructions of Zeigler and his co-workers, who would have this area as a separate plate at low latitudes. That interpretation would entail the *Neseuretus* fauna not only living under different conditions but also crossing the palaeoequator. A continuity of trilobite faunas in the Cambrian, similar to that accepted by us for the earlier Ordovician, has been argued by Chang (1980).

Position of Australia

There is considerable evidence to indicate that Australia lay within equatorial latitudes in the Tremadoc and Arenig. Graptolite, cephalopod and conodont faunas are typical of equatorial faunas elsewhere, and the platform limestones of western Queensland and other areas of the continental interior are of usual low latitude type. Arenig–Llanvirn platformal trilobite faunas have never been completely described, but are under study by J. Shergold and R. A. Fortey. Pelagic elements are the same as in other circumequatorial faunas, but the benthic faunas include a number of curious endemic genera, including a bizarre local radiation of Asaphidae. There are also a few 'Gondwanan' elements (but not *Neseuretus*) such as *Hungioides* which are known from South America, southern China, or both. It seems reasonable to accept the attachment of Australia to Gondwanaland as in the Whittington & Hughes (1974) and Scotese *et al.* (1977) maps, and accord it an equatorial position. The southern part of Argentina also presumably extended towards lower latitudes. Here should be mentioned the record of ?*Neseuretus* by Legg (1976) from the Arenig of the Canning Basin, northwestern Australia. Unfortunately these are pygidia only, of calymenacean type, and it seems more probable to us that another genus is represented; certainly the associated fauna is generally unlike that of the *Neseuretus* fauna, and the geographical position would be most anomalous.

Associated fauna

Age. Dr J. Ferguson informs us that the fossil bed with trilobites which we have examined is both overlain and underlain by graptolitic shales. It consists entirely of 'tuning fork' graptolites, among which *Didymograptus murchisoni*, *D*. cf. *geminus*, *D*. *artus* and *D*. cf. *spinulosus* were identified. This is without doubt an assemblage of Llanvirn age, and very likely within the upper Llanvirn Zone of *D*. *murchisoni*. The age of the trilobite fauna is therefore also late Llanvirnian. Broken didymograptid stipes occur within the trilobite bed itself.

Dr L. R. M. Cocks has determined three genera of inarticulate brachiopods, which occur in the same blocks as the trilobites: *Schizocrania*?, *Monobolina* and *Lingulella*. Of these, *Monobolina* is significant in being a restricted Anglo-Welsh to southern European genus, typically found in shallow water facies. The bivalves include *Glyptarca* cf. *naranjoana* (Verneuil & Barrande, 1855) (Dr N. J. Morris det.); this was originally described from Spain.

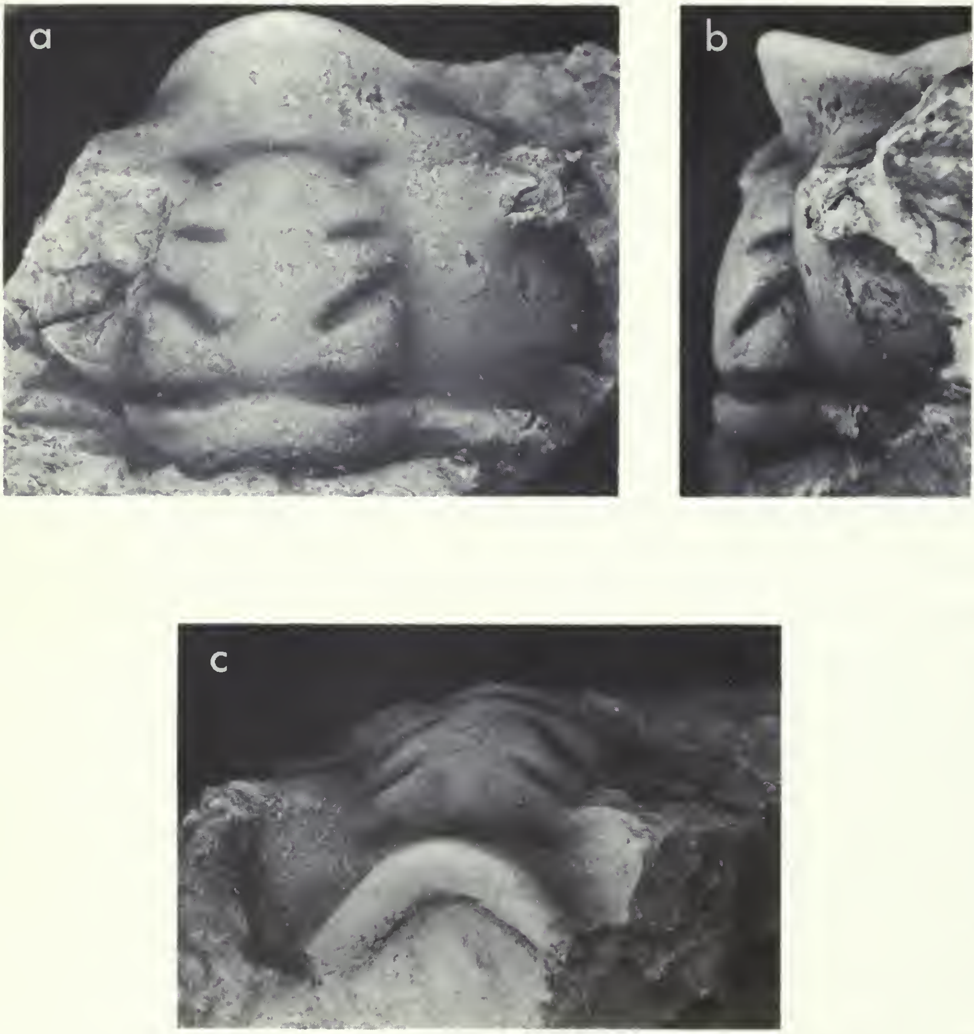


Fig. 3 *Neseuretus tristani* (Desmarest, 1817). Cranidium It.15738. Llanvirn Series, Hanadir Shale; Aṭ-Ṭīnīyāt, Saudi Arabia. a, dorsal view, ×3. b, right lateral view, ×2·5. c, anterior view, ×3.

Both the bivalve and the brachiopods are associated with the trilobite *Neseuretus* at their other localities. Together they constitute a characteristic assemblage of fossils—an inshore, low diversity fauna from clastic facies—which may be termed the *Neseuretus* fauna (*Neseuretus* community type of Fortey & Owens, 1978). Thomas (1977) described a species of the trilobite *Plaesiacomia* from a different locality in the Hanadir Shale. *Plaesiacomia* is another trilobite of restricted, boreal distribution in the earlier Ordovician (Dean 1976), but is generally found in deeper water facies than *Neseuretus*.

Lithology. Mrs J. Bevan has kindly examined the rock yielding the body fossils under the electron probe. The trilobites themselves have been replaced by an iron-rich dolomite. The rock includes mudflakes (composed of fine orthoclase, quartz and dolomite), and significant quantities of iron oxide (probably limonite) grains, set in a matrix of fine dolomite, felspar and quartz. The trilobites are entirely preserved as disarticulated parts, often densely stacked on one another. The rock is evidently a coquina.

Systematic note

Family **CALYMENIDAE** Burmeister, 1843

Neseuretus has been assigned to a separate family Synhomalonotidae Kobayashi, 1960. We accept here the arguments advanced by Henry (1980) that the hypostoma in particular indicates calymenid affinities.

Genus ***NESEURETUS*** Hicks, 1873

Type species. *Calymene parvifrons* var. *murchisoni* Salter, 1865; see Whittard 1960 : 139.

Date of authorship. The date of authorship of *Neseuretus* has been variously quoted as 1872 (Whittard 1960, Dean 1966, Dean & Martin 1978), 1873 (Henry 1980) or 1876 (Dean 1967). Hicks' paper appears in the first part of volume 29 of the *Quarterly Journal of the Geological Society of London.* Each page carries the date 'Nov. 1872', which is presumably the source of the 1872 date of publication. However, the cover page (which also includes on the reverse an account of Society business transacted early in 1873) bears the date 1873, which is the correct year of publication. November 1872 is the date of the meeting at which Hicks' paper was presented.

Species included in *Neseuretus* (*Neseuretus*).

N. antetristani Dean, 1966	Arenig; France
N. arenosus Dean, 1966	Arenig; France
N. attenuatus (Gigout, 1951)	? Llanvirn; Morocco
N. avus Hammann, 1977	early Llanvirn; Spain
N. bergeroni (Thoral, 1935)	Arenig; France
N. brevisulcus Whittard, 1960	Lower Arenig; England
N. bullatus Whittard, 1960	Lower Llanvirn; England
N. complanatus Whittard, 1960	Lower Arenig; England
N. concavus Lu, 1975	Llanvirn; Shensi, China
N. concavus tenellus Lu, 1975	Upper Llanvirn; Shensi, China
N. convexus (Sheng, 1958)	Upper Llanvirn; Szechuan, China
N. ? elongatus Hicks, 1873	Arenig; Wales
N. equalis Lu, *in* Lu & Chang 1974	Lower Ordovician; Szechuan, China
N. expansus Lu, 1975	Llanvirn; Shensi, China
N. grandior Whittard, 1960	early Arenig; England, West Germany
N. henkei Hammann, 1977	Llandeilo; Spain
N. intermedius Lu, 1975	Llanvirn; Szechuan, China
N. kayseri (Kobayashi, 1951)	Arenig/Llanvirn; Szechuan, China
N. kobayashi (Harrington & Leanza, 1957)	Llanvirn; Argentina, Bolivia

N. lusitanicus (Thadeu, 1949)	Llandeilo; Portugal
N. monensis (Shirley, 1936)	Arenig; Wales
N. murchisoni Salter, 1865*a*	Arenig; Wales, England
N. nivalis (Salter, 1865*b*)	mid-Ordovician; central Himalayas
N. pamiricus Balashova, 1966	Llandeilo; Pamirs
N. parvifrons (M'Coy, 1851)	Arenig; Wales
N. planus Lu, 1975	Llanvirn; Shensi and Szechuan, China
N. ? *quadratus* Hicks, 1873	Arenig; Wales
N. ramseyensis Hicks, 1873	Arenig; Wales
N. sanhwaichangensis Lu, 1975	Llanvirn; Szechuan, China
N. sanlucaensis Přibyl & Vaněk, 1980	Llanvirn; Bolivia
N. sexangulus Dean, 1971	Lower Arenig; France
N. shensiensis (Lu, 1957)	Llanvirn; Shensi, China
N. tristani (Desmarest, 1817)	Upper Llanvirn–Llandeilo; France, Portugal, Spain, England, Algeria
N. tristani or *parvifrons* (of Whiteman, 1971)	Llanvirn or Llandeilo; Tunisia
N. tungtzuensis (Sheng, 1958)	Upper Llanvirn; Yunnan, China
N. vaningeni Dean, *in* Dean & Martin 1978	Lower Arenig; Newfoundland
N. yinganensis [? Chang, *in* Chang *et al.* 1979]; apparently a *nomen nudum*	Caradoc; Xinjiang, China
N. zunyiensis Yin, 1978	Arenig; Kweichou, China
N. ? sp. (Dean, 1971)	Arenig; Turkey
N. sp. (Destombes, 1967)	early Arenig; Morocco
N. sp. (Destombes, 1967)	Llandeilo; Morocco
N. sp. (Henry, 1980)	Llandeilo; north-west France
N. sp. (Whiteman, 1971)	Arenig; Algeria
N. sp. nov. (Whiteman, 1971)	Arenig; Algeria
N. spp. nov. (Whiteman, 1971)	Llanvirn; Algeria
N. sp. (Dean, 1975)	Arenig or Llanvirn; Peru
N. ? sp. (Kobayashi, 1951)	Llanvirn; Kweichou, China

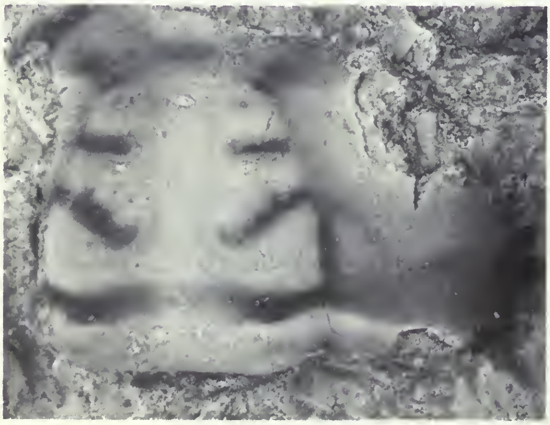
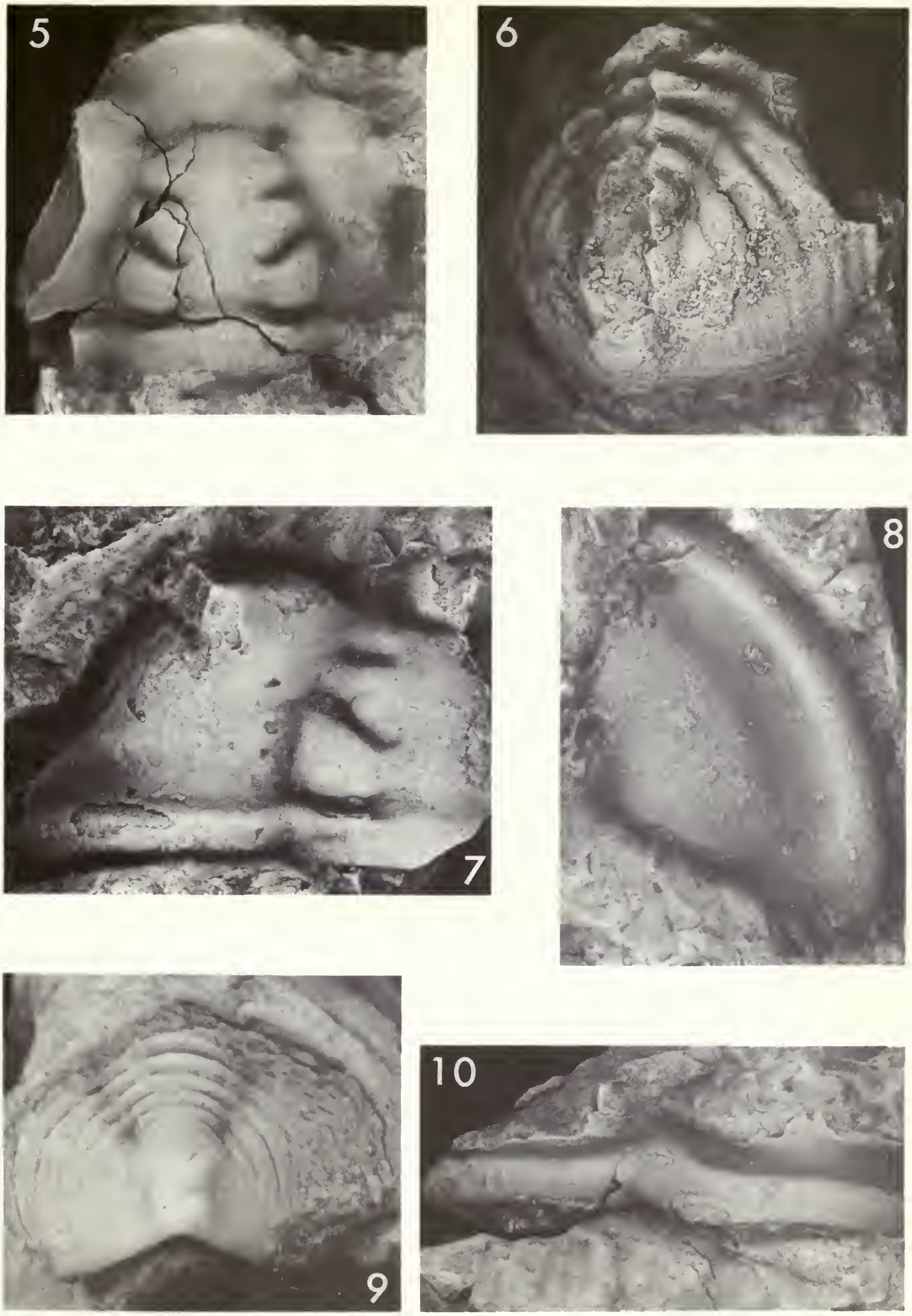


Fig. 4 *Neseuretus tristani* (Desmarest, 1817). Cranidium It.15740, dorsal view, ×3. Llanvirn Series, Hanadir Shale; Aț-Țīnīyāt, Saudi Arabia.

Neseuretus tristani (Desmarest, 1817)
Figs 3–11

Although usually attributed to Brongniart (1822) there is a valid proposition of the species in Desmarest (1817 : 517). Desmarest uses the name with reference to a Brongniart work in preparation, but this does not have formal status. For subsequent synonymy see Henry (1970, 1980) and Sadler (1974).



Figs 5–10 *Neseuretus tristani* (Desmarest, 1817). Llanvirn Series, Hanadir Shale; Aṭ-Ṭīnīyāt, Saudi Arabia. Fig. 5, dorsal view of small cranidium It.15739, ×3. Fig. 6, dorsal view of pygidium It.15748, ×3. Fig. 7, dorsal view of fixed cheek It.15741, ×2·5. Fig. 8, free cheek It.15742, ×3. Fig. 9, posterior view of pygidium It.15744, ×2·5. Fig. 10, portion of thoracic segment It.15743, ×3.

MATERIAL. More than fifty fragments of this species were recovered, of which the following are registered in the collections: cranidia: It.15738–41; free cheek: It.15742; thoracic segment: It.15743; pygidia: It.15744–48.

LOCALITY AND HORIZON. Aţ-Ţīnīyāt, Jabal Shammar, northern Saudi Arabia; 27° 41′N, 42° 20′E. Llanvirn Series, Tabuk Formation, Hanadir Shale, Zone of *Didymograptus murchisoni.*

REMARKS. This species has been extensively revised by Henry (1970, 1980) and Sadler (1974) and further description is unnecessary. It is possible to match every feature given in Henry's recent, careful and well-illustrated account in the Saudi Arabian material. The lateral cranidial profile is identical, with the long frontal border relatively steeply upturned, compared with the British species of Arenig age (Henry 1970 : fig. 2). The only species of Llanvirn age from Britain, *N. bullatus* Whittard, 1960, has a short frontal area, like *N. vaningeni* Dean, *in* Dean & Martin 1978, from the Arenig of eastern Newfoundland. The vaulting on the cranidial border is particularly marked in *N. tristani.* We have obtained specimens (see Fig. 4) which show the muscle insertion areas and fine granulation clearly on the external surface; these compare closely with the specimen in Henry (1980 : pl. 10, fig. 3). Some of the other specimens from Saudi Arabia (Fig. 3) appear to be almost without granulation; we regard this as an intraspecific variation only. Other species of *Neseuretus* do not appear to have defined 1P muscle insertion areas, which are prominent on some specimens of *N. tristani.* The deflexion of the 1P glabellar furrow around the back of this muscle insertion area presumably accounts for the sigmoidal form of 1P in many Homalonotidae and Calymenidae. We note one small difference on pygidia of our material compared with the descriptions of Henry (1970, 1980); Henry describes as many as nine axial rings in total, of which the first six or seven pass across the mid-part of the axis. No more than six axial rings are defined across the mid-part of the axis on Arabian specimens, with up to two more faint impressions on the terminal piece. In other respects, such as sculpture and relative definition of pleural and interpleural furrows, the French specimens are so similar to ours that we cannot consider a specific distinction on the basis of this pygidial difference alone. The Arabian form is also close to the species identified as *N. birmanicus* (Reed) from Yunnan by Sheng (1974 : pl. 8, figs 2a–g) which differs mainly in having a weakly defined cranidial rim or border. Dean (1967) assigned *N. birmanicus*, *sensu stricto*, to his subgenus

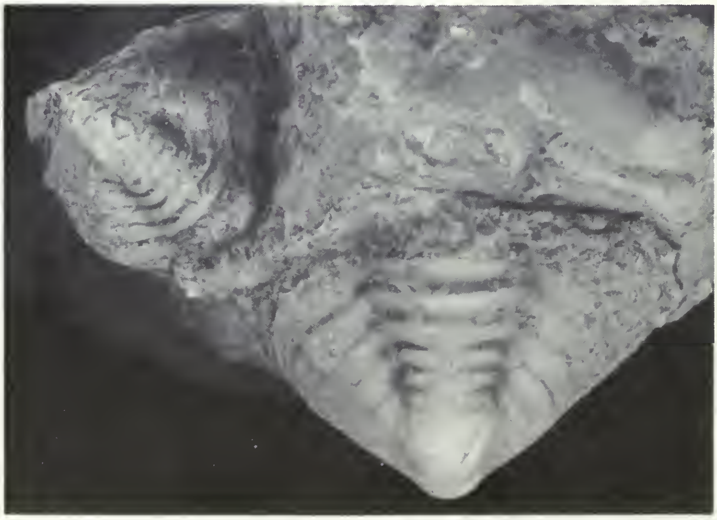


Fig. 11 *Neseuretus tristani* (Desmarest, 1817). Dorsal view of pygidium It.15744, ×2·5. Llanvirn Series, Hanadir Shale; Aţ-Ţīnīyāt, Saudi Arabia.

Neseuretinus on the basis of a defined cranidial border. The material illustrated by Sheng includes (1974 : pl. 8, fig. 2d) specimens with a border no better defined than that of the type species of *Neseuretus*, *N. murchisoni* (compare Whittard, 1960 : pl. 20, fig. 14), and the Yunnan species should evidently be placed in *Neseuretus* in a restricted sense. We conclude that *N. tristani*, together with what may be very closely related species, extended over much of Gondwanaland in the Llanvirn.

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Archaeocidaris whatleyensis sp. nov. (Echinoidea) from the Carboniferous Limestone of Somerset, and notes on echinoid phylogeny

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Synopsis

The new species *Archaeocidaris whatleyensis* is described from the Carboniferous Limestone of the eastern Mendip Hills of Somerset, England. The specimens came from the Clifton Down Limestone of Holkerian age, and their preservation suggests that they were buried rapidly.

The phylogenetic position of the species with respect to more advanced echinoids is discussed, using a cladistic approach. *Archaeocidaris* is seen as part of the stem group of all echinoids. *Miocidaris* probably includes stem echinoids, stem cidaroids and stem euechinoids; the echinothurioids are the primitive sister group to all other euechinoids.

Introduction

Field-work by R. Shaw in Whatley Quarry, Whatley, near Frome, Somerset (Nat. Grid ref. ST 727480) in April 1977 produced a well-preserved specimen of *Archaeocidaris* (E.76887; all specimens prefixed E are in the BM(NH), see p. 81. One of us (P.C.E.) revisited the quarry during the summer of 1977 and collected further specimens (E.76888, E.76889) from the same place in the quarry. A preliminary note on this material appeared in 1978 (Ensom 1978).

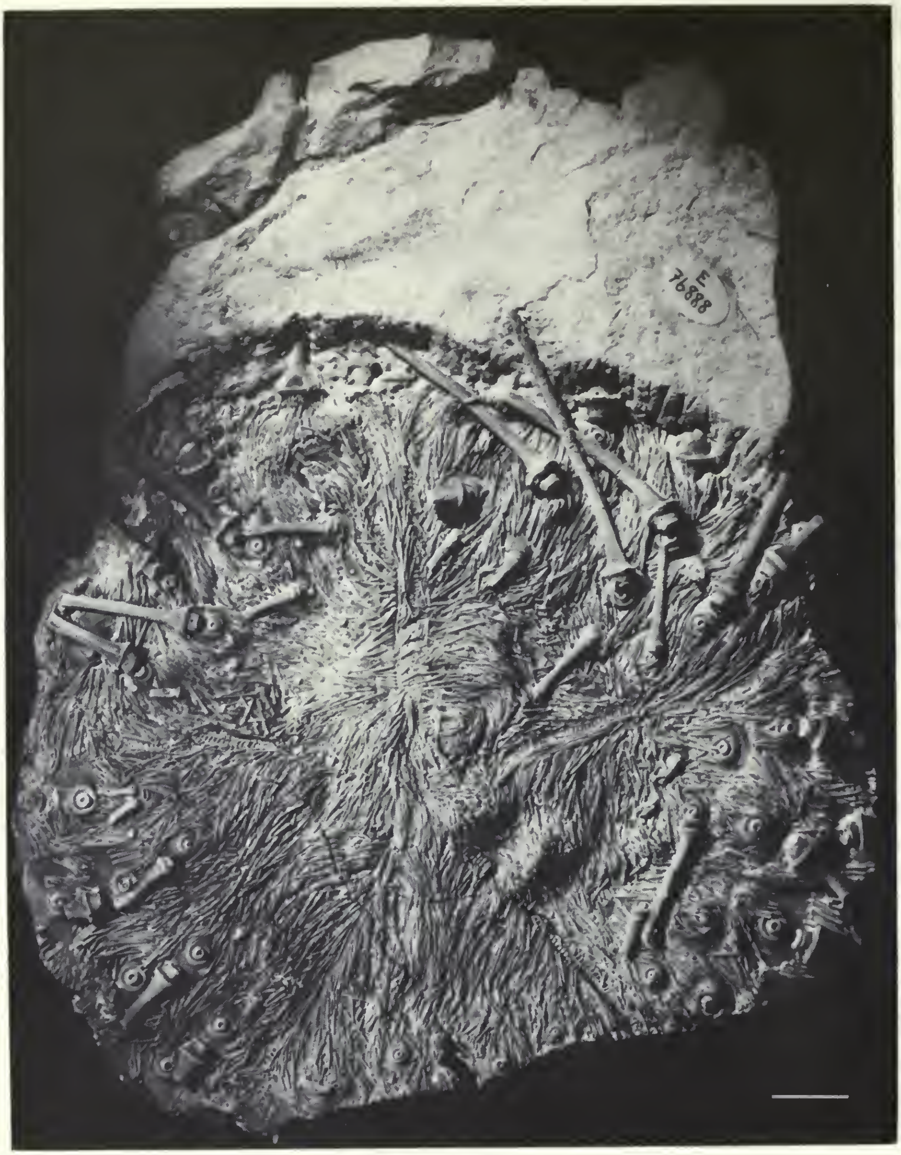
All the specimens came from fallen blocks of deeply weathered Carboniferous Limestone, found near each other. Specimen E.76887 was embedded in a calcareous silt; specimen E.76888 came from a silty calcilutite which contained the carbonized remains of small non-calcareous algae along bedding planes. The algae are identified as dasycladacean (? Chlorophyta; Elliott 1982 herein). Elliott makes a comparison with the fossil *Archaeobatophora* Nitecki (Ordovician) and *Inopinatella* Elliott (Silurian), and with the living shallow-water marine *Dasycladis* and *Batophora*: see p. 106.

This paper describes in detail the new species *Archaeocidaris whatleyensis* and discusses the phylogenetic position of *Archaeocidaris* with respect to more advanced echinoids.

Palaeozoic echinoids are rather rare, particularly those which are well preserved and nearly complete (Kier 1965). The holotype of the new species *A. whatleyensis* is especially well preserved, with many pedicellariae present, as well as the jaw apparatus and primary, secondary and miliary radioles. The paratype E.76887 displays features which are hidden or missing in the holotype. Perhaps the most interesting of these features are the remains of two compasses, comprising two outer portions and two inner portions. One of the most important features present on the holotype and on an isolated demipyramid (E.76899) is the very tuberculate nature of the demipyramid/epiphyseal suture faces. This tuberculation is present on *A. nerei* (BM(NH) 32846 and E.9328), and probably on other species of *Archaeocidaris*.

Bull. Br. Mus. nat. Hist. (Geol.) **36** (2): 77–104

Issued 28 October 1982



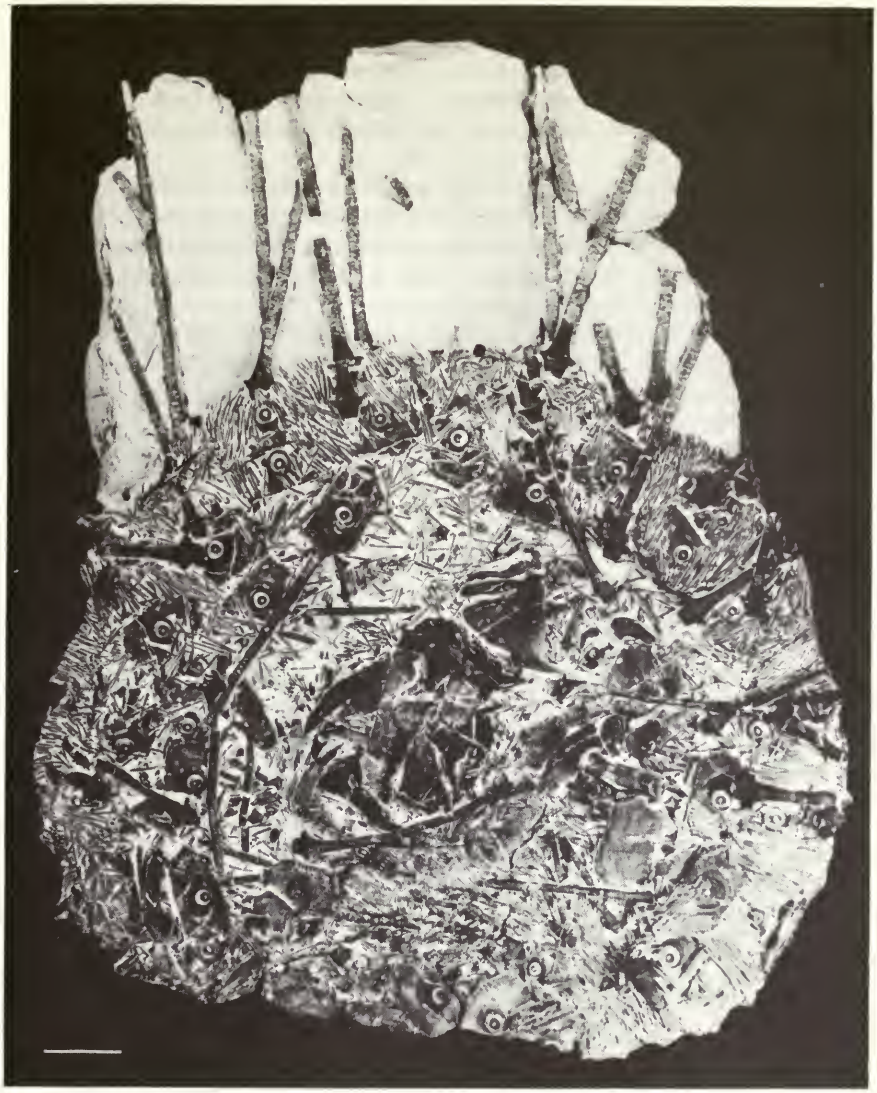
1a

Fig. 1a Apical surface of the holotype, E.76888.

The extensive work by Jackson (1912) described three species of *Archaeocidaris* in which the test is at all complete, *A. wortheni*, *A. rossica* and possibly *A. urii*. Unfortunately, Jackson did not describe the specimens in great detail.

Archaeocidaris is important to the phylogeny of more advanced echinoids. Euechinoids have features which are present in *Archaeocidaris* and which are usually regarded as advanced characters, such as hinge-joint lanterns, and foramina magna deeper and broader than the shallow foramina magna of cidarids. The lanterns of cidarids are socket-jointed, which is an advanced character.

Archaeocidaris is a stem echinoid. The classification used in the *Treatise* (Fell 1966) is mistaken to include *Archaeocidaris* with the Cidaroida. The taxon Perischoechinoidea is



1b

Fig. 1b Oral surface of the holotype, E.76888.

rejected as it is paraphyletic. Instead, the classification has to indicate the relationship by use of Hennigian terminology.

Preservation and stratigraphy

The tests of E.76887 and E.76888 were flattened after death. The additional apparently three-dimensional specimen E.76889 was recovered with the second specimen (E.76888) together with elements of other tests. We believe that E.76889 was flattened and then rolled up.

Trilobites collected from near where the echinoid specimens were found belong to the species *Linguaphillipsia matthewsi* (Hahn & Hahn) (identification by R. M. Owens, personal communication). *Linguaphillipsia* was first recorded in western Europe at Holwell Quarry, 3 km south of Whatley, on the southern limb of the Beacon Hill pericline (see Hahn & Hahn, 1973). Hahn & Hahn identify the horizon as low in the Clifton Down Limestone, Holkerian stage.

The echinoids were only partly exposed when recovered. Their development was facilitated by the relative softness of the matrix, which may be explained by a high proportion of silt in the limestone and the proximity of major solution features, including caves. Water appears to have been responsible for the partial decalcification or rotting of the limestone without affecting the specimens very much.

The exposed aboral surface of E.76888 was cleaned initially using a pin, brush and water. The exposed oral surface of E.76887 was cleaned initially by minimal use of an air-abrasive machine. The oral surface of E.76888 and the aboral surface of E.76887 required complete excavation from the matrix. Excess rock was removed from E.76887 with the aid of a diamond saw. The air-abrasive unit was then used on both specimens to reveal the remarkable detail.

Mode of preservation

The fact that two of the tests remained largely intact after death demands consideration.

Echinoids with rigidly sutured tests have a greatly increased chance of preservation in the fossil record over those with flexible tests, such as *Archaeocidaris*, which are more likely to disintegrate after death. The apical surface of E.76888 suffered little disarticulation; the primary and secondary radioles and pedicellariae have been flattened against the test, but their proximal ends remain close to their tubercles. The Aristotle's lantern remains, somewhat dissociated, in a central position. Most of the primary radioles are in contact with or lie near their corresponding tubercles. Secondary radioles are present on most plates though often displaced. A perignathic girdle is not present and never existed; however, peristomial plates are present. Unfortunately, no sedimentological information was present to indicate which way up the specimen had been buried.

The primary radioles on the adapical surface of the holotype have an approximately radial orientation, with a slight bias towards ambulacrum III or interambulacrum 3. On the adoral surface the orientation is mostly radial but the radioles at the ambulacrum III end of the test point outwards from it, almost parallel to each other. The secondary radioles are almost *in situ*, laid flat.

Most of the tips of the secondary radioles point towards interambulacra 3, 4 and 5. In interambulacra 2 and 3 some of the tips point towards the anterior ambitus. A further exception is in ambulacrum III where the shafts are parallel to the perradial suture. The adoral surface has been disrupted. This, together with the perfect preservation of the apical surface, suggests that the specimen was turned over, perhaps by a sudden influx of sediment which also suffocated the animal. The preservation of the delicate algal remains seems to confirm a rapid rate of sedimentation. The peristomial plates and the lantern collapsed into the body cavity, and minor disruption of the coronal system of the oral surface also occurred before burial of the test was complete.

The test of E.76887 is skewed. Primary radioles are almost completely absent, and secondary radioles are comparatively few. Secondary radioles are almost completely absent on the oral surface, and most of them form a confused mat on the aboral surface, though even here a significant portion of the test lacks them. Four interambulacral plates within this area are damaged. Two of them have only scars to indicate that a mamelon was present, and a deep groove crosses one of these. There is no disarrangement of the plates. Perhaps this represents damage inflicted by a predator. The matrix from which the specimen was extracted has geopetals and small-scale sedimentary structures (cross-bedding) which show that the specimen was buried upside down. The layer in which it was buried rests on a poorly-sorted, silty microbiosparite containing crinoid, coral and brachiopod-shell debris as a coarse component. The matrix surrounding the specimen is a calcareous terrigene which is fine-grained and streaky in appearance with some small-scale cross-bedding. This suggests that an influx of sediment-laden water may have been partly responsible for the preservation of this specimen, though lack of spines and some disarticulation indicates a time lapse between death and final burial. In acroechinoids the lantern is frequently missing, or is very fragmentary, despite the possession of a rigid test which enhances the chance of fossilization (Smith 1981). This indirectly confirms that the new archaeocidarids were buried rapidly.

In both specimens the presence of much silt in the matrix can be demonstrated by treating samples with hot and cold dilute hydrochloric acid. The matrix of E.76887 had so high a terrigene content that a cube of rock remained intact after the carbonate had been removed by the acid. George (1972), in his discussion of Carboniferous Limestone lithologies, mentions the occasional input of terrigenes which he relates to the influence of St George's Land to the north. The greatest influence of St George's Land is marked by the deposition of the sandstone units of the Forest of Dean area during the Arundinarian and Holkerian stages. Perhaps exceptional conditions caused mud from St George's Land to be deposited even so far south as Whatley.

Such exceptional conditions may have smothered laterally extensive colonies of *Lithostrotion* which are common on bedding planes within the Clifton Down Limestone (Green & Welch 1965); these corals are well exposed in the adjoining Lime Kiln Hill Quarry. These conditions would also account for the sudden death of the Archaeocidarids at Whatley Quarry. Similar events affected the Lower Avonian Limestones, killing crinoids *en masse* (George 1972 : 233).

Systematic description

Class **ECHINOIDEA** Leske, 1778

Family **ARCHAEOCIDARIDAE** M'Coy, 1844

Genus ***ARCHAEOCIDARIS*** M'Coy, 1844

Archaeocidaris whatleyensis sp. nov.
Figs 1–19[1]

DIAGNOSIS. The primary interambulacral radioles have an approximately triangular cross-section with a row of spinules along the two base edges of the triangle.

MATERIAL. There are three almost complete tests and sundry fragments from these, and fragments from other disintegrated tests. The **holotype** is E.76888 (Figs 1a, 1b, 3a, 3b), with two paratypes, E.76887 (Figs 2a, 2b, 5a, 5b) and E.76889 (Fig. 6). All the specimens are in the collections of the Department of Palaeontology, British Museum (Natural History).

The specimens are from the Lower Carboniferous, Dinantian, Holkerian Stage, Clifton Down Limestone, from Whatley Quarry, near Frome, Somerset (National Grid ref. approx. ST 727480). E.76888 and E.76889 were collected and presented by P. C. Ensom; E.76887 was collected and presented by R. P. Shaw.

SHAPE. All the specimens have been flattened dorsoventrally. The shape of the living animal is unknown, but was probably an oblate spheroid. The holotype, E.76888, is 107 mm across its broadest part, excluding radioles, and has a domed central area on the apical surface where the test has collapsed over the Aristotle's lantern. The paratype E.76887 is 82 mm across its widest part, and paratype E.76889 is 40 mm across its widest part. E.76889 is about 20 mm tall, but this is because the specimen had been rolled up. All specimens have suffered some plate displacement.

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[1] Scale bar represents 10 mm, broken scale bar represents 5 mm.

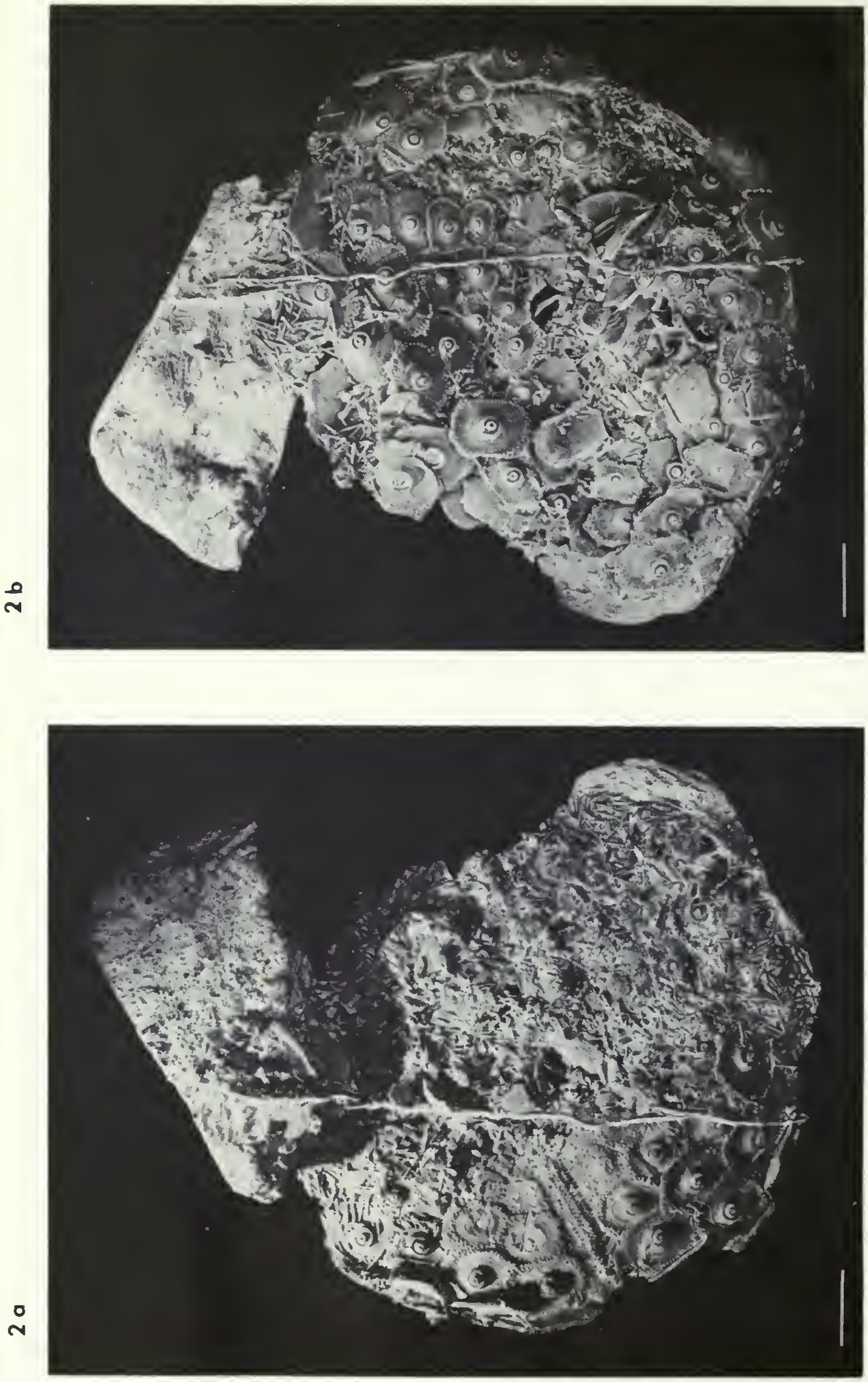


Fig. 2 Paratype E.76887. a, apical surface. b, oral surface.

Apical system (1). Ocular plates. No plates on any of the specimens can be positively identified as ocular plates. The apical surface of the holotype is covered by secondary radioles. By following the course of the ambulacra adapically, the approximate positions of the ocular plates can be determined. Several small tubercles can be seen in this position, with small radioles lying scattered adjacent to the tubercles, as seen at ambulacrum III.

(2). Genital plates and madreporite (Figs 7, 8, 17a). The genital plates cannot be positively identified because of the disrupted state of the tests of the paratypes and the spine cover of the holotype. However, on paratype E.76887 there are two plates which are probably genital plates. One of these is present on interambulacrum 5, seen from the adapical surface, and is situated at the adapical end of the interambulacrum which it terminates (Fig. 7). Its margins are mostly obscured by other plates and test debris, but in position Va the margins can be seen. The transverse margin is curved so that it follows the adjacent edge of the interambulacral plate. Adoral to the curve there is a flange to imbricate with the interambulacral plate. The lateral margin is convex and has no flange. The apical transverse margin is hidden by periproctal plate debris. The adradial margin is convexly curved the whole of its length. In the adoral position of the mid-line of the plate, there is a hole which may be the genital pore. It has an elliptical outline, with the long axis following the mid-line. Plate ornament consists of a few randomly distributed small tubercles. One of these is present on the adoral margin of the genital pore, growing into the pore. The plate is 5 mm long.

The second probable genital plate is present on the oral side of the specimen in interambulacrum 1, with the inner surface of the plate visible. The shape is rather like a square with one corner removed leaving a third of one side of the square and two-thirds of another. The genital pore is circular and is situated near the margin of the side of the square nearest the mouth. The plate has a smooth surface and is 4·5 mm long.

The madreporite is present on the holotype (Fig. 8) and on paratype E.76887. It appears to be *in situ* on the holotype, but as most of it is masked by small radioles, we cannot be sure. On the paratype it is present on the apical surface, and is not *in situ*, but still remains in interambulacrum 2. It is about 6 mm long and about 4·5 mm wide. The narrower ends are obscured by test debris. The plate appears to be bilaterally symmetrical about the greater dimension. The margin has a flange around it which is interrupted in at least four places. The plate above and within the flange is convex and has several small tubercles randomly distributed, and many tiny pores over the whole of the surface. On the madreporite of the holotype the tubercles bear small radioles.

(3). Periproct. This is not visible on the holotype nor on the paratypes. However, on paratype E.76887 there are several small plates on the apical surface which are probably periproctal plates. They each are irregular in outline and have ornament consisting of tubercles arranged in a regular, concentric fashion on some of the plates. On the holotype the area occupied by the periproct is covered by small radioles, indicating that the tubercles on the paratype E.76887 also bore radioles.

Ambulacra (Figs 7, 10, 20b, 21). The ambulacra are faintly sinuous, almost straight. Each ambulacrum consists of two rows of simple plates with no suggestion of compounding. The paratype E.76887 shows ambulacrum I extremely well from the apical surface. It is about 5 mm wide, from the adapical end to the ambitus where it is totally disrupted. The width of the interambulacrum at the ambitus is 40 mm, so that the width ratio of ambulacrum to interambulacrum is 1 : 8 at the ambitus. This ratio alters towards the apical system where the ambulacral width remains the same but the interambulacral width decreases. Each ambulacral plate is wide and low. The pore pairs as seen from the outer surface are almost centrally placed, slightly perradial. The pores of a pair are unequal. The perradial pore has an elliptical outline while the adradial pore is comma-shaped and larger. Both pores have their long axes parallel to the width of the plate. Each pore is surrounded by a slightly raised wall which joins between them and forms an adorally pointing projection. Adapical and adoral to the projection is a long, low, triangular pit. The inner walls of each pore are steep and smooth and are parallel to the radius of curvature at each pore.

The ornament of the outer surface of each ambulacral plate consists of between three and five small tubercles. The plates with three tubercles are found near the apical system; those with five are found where the ambulacral plate expands adradially into the V-shaped junction on the adradial margins between two adjacent interambulacral plates.

All the ambulacral plates have two tubercles on their perradial parts – one central marginal tubercle and one inner tubercle close to the adoral perradial suture. This suture sometimes truncates the inner tubercle.

The ambulacral plates imbricate adorally by means of flanges and bevels, and steeply sloping adoral and adapical margins (Figs 20b (p. 94), 21 (p. 95)). Each plate has a broad, approximately triangular flange on the adapical-adradial end. The flange tapers perradially to disappear by the adradial pore. The flange is expanded on some plates adradially at the V-shaped junction between two interambulacral plates. The flange reappears by the central projection and expands adapically and perradially to a level with the adapical part of the inner tubercle. On the underside of each plate there is a corresponding bevelling on the opposite side to the flange, so that each ambulacral column can imbricate. The adoral margin of an adapical plate imbricates over the adapical margin of its adoral neighbour and the adoral perradial margin of one plate imbricates over the adapical perradial margin of its adjacent neighbour. The interambulacral plates are able to imbricate perradially over the ambulacral plates.

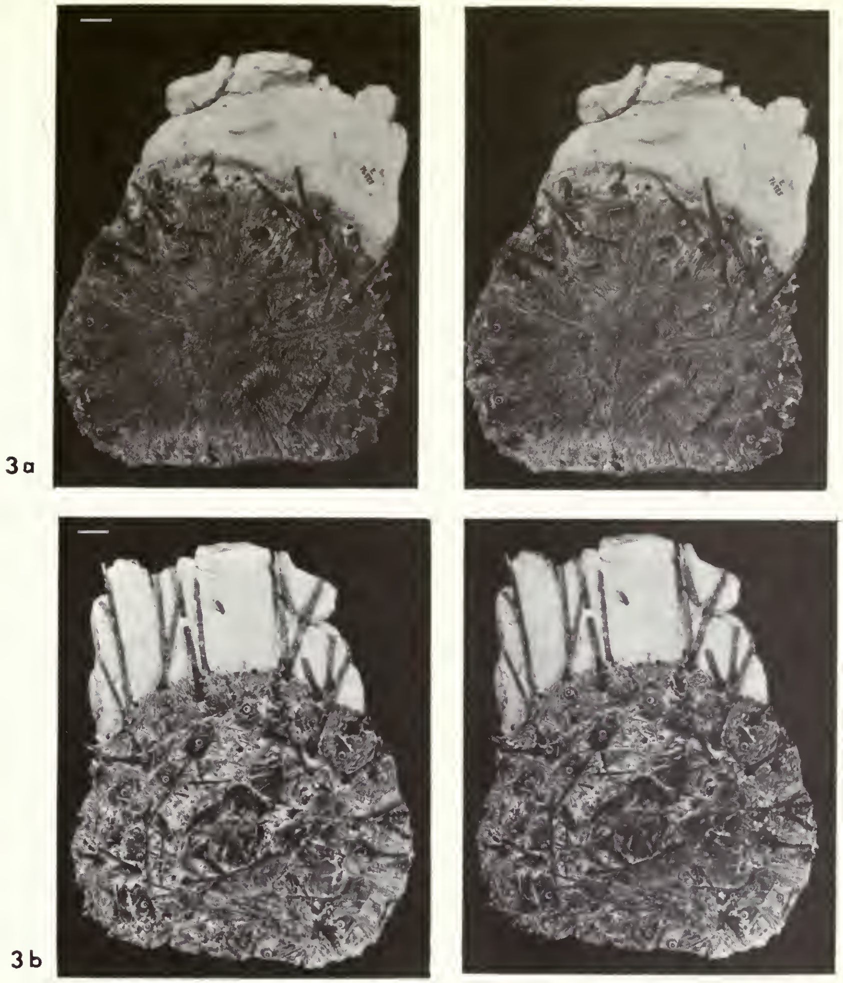
INTERAMBULACRA (Figs 7, 9, 12, 15a, 15b, 20a (p. 94), 22 (p. 97)). There are four columns of plates to each interambulacrum. Most plates bear a single, large, perforate tubercle, surrounded by scrobicular tubercles.

The arrangement of the interambulacra is best seen in specimen E.76887, where the spines have been lost, and the columns on both the adapical and adoral surfaces are clearly visible. The interambulacra of the holotype are obscured by small spines over the adapical surface and are disrupted on the adoral surface. Description of the interambulacra is therefore based on the paratype E.76887, on interambulacra 1 and 5 of the adapical surface, and 1–4 of the adoral surface.

The interambulacral plates are wider than tall, larger at the ambitus, and decrease in size adapically and adorally. The plates on the adoral surface all bear large primary tubercles, but the plates of the adapical surface (see Fig. 7) have no large primary tubercles on the first two horizontal series. The plates without large primary tubercles have central swellings with widely spaced concentric scrobicular tubercles over the remaining plate. The plates with large primary tubercles have scrobicular tubercles also.

Each primary tubercle (see Fig. 12) is in the centre of the plate. It has a very low basal terrace with a broad oval outline. The circular, gently concave boss rises steeply and is slightly tilted, with the shallower slope on the adoral face. At the top is a high, thick parapet. The platform is flat and about the same width as the parapet rim. Some plates have a slight excavation on the adoral and adapical sides. The mamelons have straight necks, and are either hemispherical, or cylindrical nearer the peristome. The foramen in either case is deep and has either a circular or a D-shaped (or sometimes kidney-shaped) outline. Where the foramen is D-shaped and the platform deep it is likely that the radioles moved mainly parallel to the long axis of the foramen. The plates of the two inner interambulacral columns are hexagonal and the plates of the outer two columns are pentagonal, with the adradial margin more or less convexly curved (Fig. 7).

Secondary tubercles are present on all interambulacral plates. Details of structure have been lost owing to slight abrasion or decalcification of the test. However, it shows the small tubercles each to have a convex boss, no parapet and a rounded imperforate mamelon arising from the boss. There is one complete ring of tubercles around the scrobicule of each primary tubercle. At the adradial and interradial ends the plate develops further rows of tubercles which would form up to four rings of tubercles if the plate was wide enough. Radiating from the basal terrace across the scrobicule are weak plications. Each plication has at its proximal end a secondary tubercle of the first ring. The subsequent incomplete rings of tubercles may



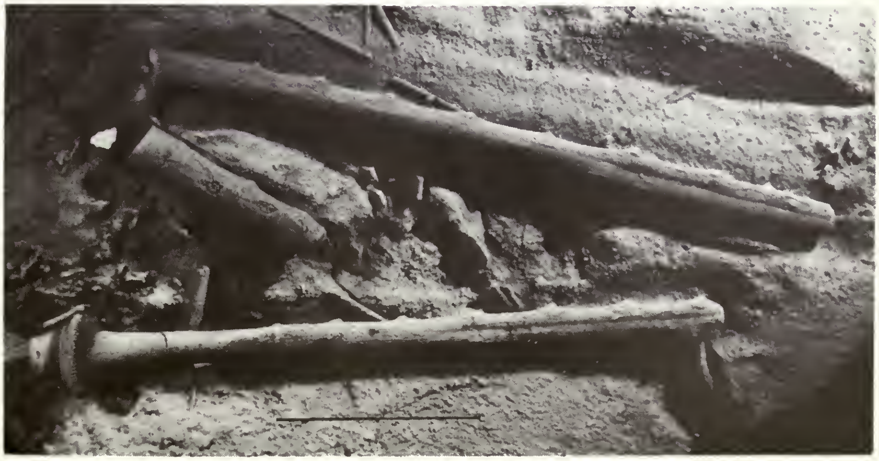


Fig. 3 Stereo-photographs of the holotype, E.76888. a, apical surface. b, oral surface.

Fig. 4 Primary radioles of the holotype, E.76888, showing spinules and crushed distal ends.

alternate behind the first or may be situated directly behind the first – there is no constancy in this arrangement.

The secondary tubercles protrude over the plate margin to give a scalloped appearance to the plate. This is especially noticeable on the adoral surface of paratype E.76887. The tubercles of one plate interlock with those of its neighbours (Fig. 9). The adradial plate margins of the two outer columns of interambulacral plates interlock with the adradial margins of the adjacent ambulacral plates.

Along the adoral margin of each interambulacral plate there is a flange which continues around the adoral interradial margin (Figs 12, 20a, 22). The outer columns of plates have flanges on the adapical interradial margins, but the inner two columns of plates do not (Fig. 12). The facet on the internal surface at the edge of the adradial margin of each outer plate is smooth and concave and imbricates over the adjacent ambulacral plates. The adoral adradial and adapical adradial margins of the inner columns of plates have narrow facets and shallow grooves undercutting the tubercles of the plate margins. The adapical margins of the outer and inner columns have similar facets and grooves. This arrangement allowed the plates, in life, to flex slightly about the contacts as a hinge. On contraction of the assumed meridional muscles, the curvature of the test would be increased, by one margin rotating over an adjacent margin. Measurements for a typical interambulacral plate from near the ambitus of the holotype and paratype E. 76887 are:

	Holotype E.76888	Paratype E.76887
Width (parallel to horizontal sutures)	13·0 mm	11·0 mm
Height (perpendicular to horizontal sutures)	9·2 mm	7·0 mm
Height of tubercle (scrobicule to mamelon)	2·0 mm	1·8 mm
Diameter of mamelon	1·5 mm	0·9 mm
Maximum length of foramen	0·5 mm	0·2 mm

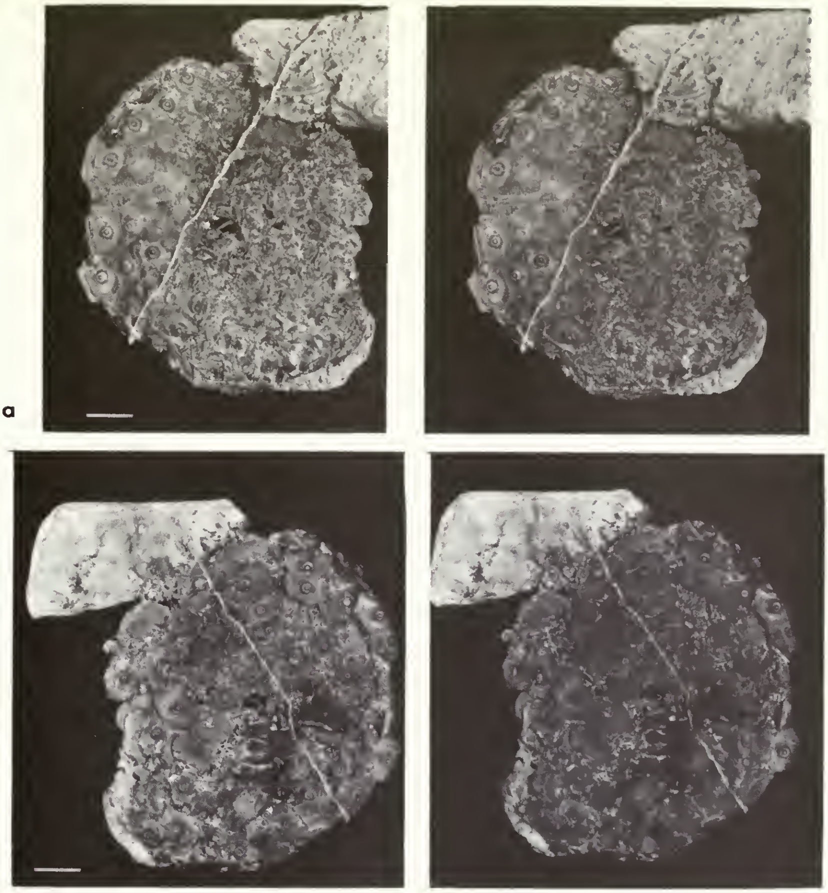
The holotype has at least seven plates per column, some obscured by spines. The paratype E.76887 has at least nine plates per column.

Certain interambulacral plates of the holotype are slightly unusual. One such plate is present on the adoral surface at interambulacrum 1 (Fig. 15a). It has secondary tubercles on the surface of the scrobicule, and four or five on the basal terrace and lower boss. The boss has steep, convex sides. On the top of the adoral side are two small tubercles in shallow hollows. In the centre of the boss is a trilobed perforate mamelon with a platform aboral to it. The plate is 10 mm wide and about 5·5 mm tall.

Other unusual plates are seen on the adapical surface of the holotype and are the first ones of the interambulacral columns to bear tubercles. They can be seen in interambulacra 4 and 5. The plate in interambulacrum 4 is mostly covered by secondary radioles but the primary tubercle is exposed. It has no basal terrace, the boss is low and convex and the mamelon arises directly from the boss. The mamelon is very elongate – 1·3 mm long, 0·5 mm wide – and forms a thin wall around a correspondingly elongate foramen. The wall rises gently to a sharp edge in the middle of the longer sides. There are two primary radioles lying very close by, almost in contact with the mamelon. They probably belong to the tubercle (Fig. 15b).

There is a variation in the distribution of tubercles with D-shaped foramina between the holotype and the paratype E.76887. The latter has the first five or so tubercles, from the apical surface to the ambitus, with D-shaped foramina. The long axis of the D is parallel to the ambitus. The remainder of the tubercles have circular foramina. The holotype has circular or just oval foramina from the apical surface to the ambitus. Adoral tubercles have circular foramina. Paratype E.76889 also has D-shaped and circular foramina.

PERISTOME AND ARISTOTLE'S LANTERN (Figs 16a–d, 17b, 18a–b, 19a–c). None of the specimens has the entire peristome preserved. However, the holotype and paratype E.76887 have most of the lantern present. The holotype has some peristomial plates. Other fragments of lantern – E.76899 (Figs 18a–b), E.76900 (Figs 19a–c) – come from other specimens of the



5a

5b

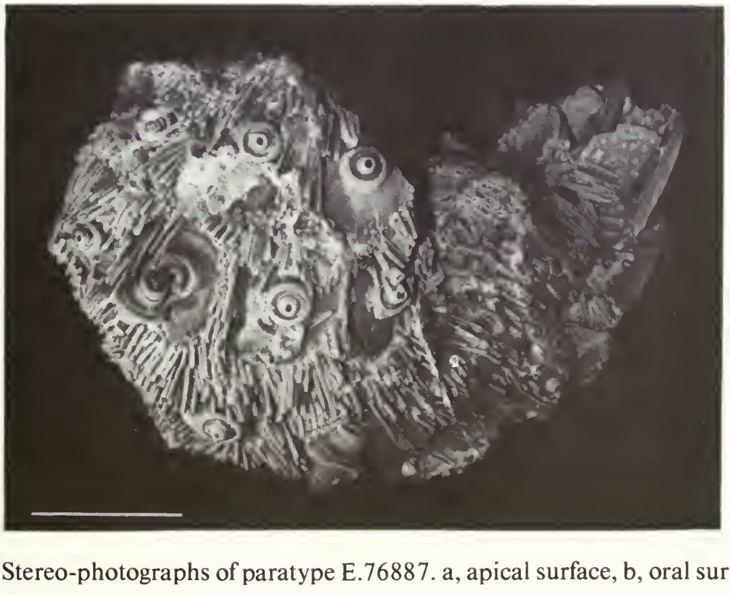


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Fig. 5 Stereo-photographs of paratype E.76887. a, apical surface, b, oral surface.
Fig. 6 Paratype E.76889.

same species from the same locality and serve to clarify the morphology of the lanterns of the more complete specimens.

(1). Peristome border. Only one plate on paratype E.76887 probably came from the peristome border. This plate is present within the area of interambulacrum 5 on the oral side. It has basically the same structure as the other interambulacral plates, with a tall cylindrical mamelon with circular foramen. It differs from other plates in having one horizontal margin truncated as far as the basal terrace, probably by resorbtion at the edge of the peristome. There is no indication of apophyses or other muscle attachment points for the control of the lantern.

(2). Peristomial plates (Fig. 16d). These are scattered over the adoral surface of the holotype, and in the area around interambulacrum 3 there are seven ambulacral peristomial plates lying close together and imbricated with each other. Each ambulacral peristomial plate consists of a long, curved, projecting part, with a large expanded blade at one end and a small blade at the other. The expanded blade is adradial, the smaller blade perradial. There are two shallow pits adoral to the part where the projection joins the expanded blade. By comparison with living echinothurioids (see Sarasin & Sarasin 1887–93) the adradial expanded blade probably served for the attachment of peristomial muscles. The outer surface has a row of tubercles along the adoral edge. These bear small spines, some of which remain almost in life position.

The peristomial plates imbricate orally. When seen from the outside, the oral edge of a plate overlaps the aboral edge of its oral neighbour. Interradial peristomial plates are less readily recognized, but are probably represented by several irregularly-shaped plates on the adoral surface of the holotype, with smooth inner surfaces and with tubercles on the outer surface. These plates are much smaller than the ambulacral peristomial plates. Typical measurements for one of each are:

ambulacral peristomial plate	length of expanded blade-shaped part	2·7 mm	5·2 mm
	length of projection	2·5 mm	
interradial peristomial plate length		1·5 mm	

(3). Aristotle's lantern (Fig. 16a). a, Demipyramids. There are thirteen demipyramids visible on the adoral surface of the holotype, the three extra ones being due to the inclusion of fragments of the test of another individual of the species. Six demipyramids are visible on the adoral surface of the paratype E.76887.

An isolated demipyramid, E.76899 (Fig. 18a, 18b), belongs to neither E.76888 nor E.76887. The holotype has two pairs of demipyramids juxtaposed to form two complete pyramids, seen in interambulacra 3 and 4. The other demipyramids lie scattered nearby. All the demipyramids of the paratype E.76887 are scattered over the adoral test.

Each demipyramid is wide (pyramidal suture to wing edge), deep (outside to inside) and short (top to bottom). Each has a wide and fairly deep foramen magnum, with a shallow-angled concave side. The retractor muscle scar is a deep groove, broad and V-shaped. The deepest part of the groove is about halfway along the length of the demipyramid, shallowing towards the upper surface of the demipyramid. The angle of the scar is 30°.

Fig. 7 Part of paratype E.76887 showing the imbrication of the ambulacra, the overlapping of displaced interambulacral plates. The genital plate (g), secondary radioles, D-shaped foramina of the interambulacral primary tubercles and the inner portion of a compass (ic) are also shown. The plates at the ambitus show facets on the adapical margins of interambulacral plates, and on the surface of interambulacral plates there are radial striations.

Fig. 8 The madreporite of the holotype, E.76888, mostly hidden by secondary radioles.

Fig. 9 Interambulacral plates of E.76887 showing the interlocking of secondary tubercles. Radial striations on the plate surface are visible.

Fig. 10 Part of an ambulacrum of the holotype, seen from the inner surface of the test.

Fig. 11 Base of a primary radiole of paratype E.76889 showing an infilled centre.

Fig. 12 An interambulacral plate from E.76887 showing two adoral flanges (af).

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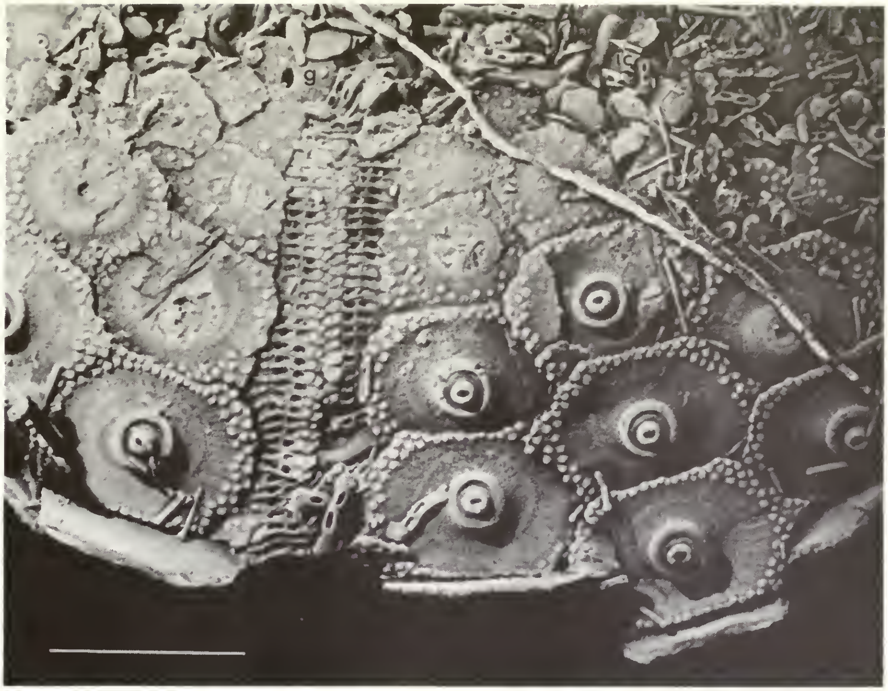

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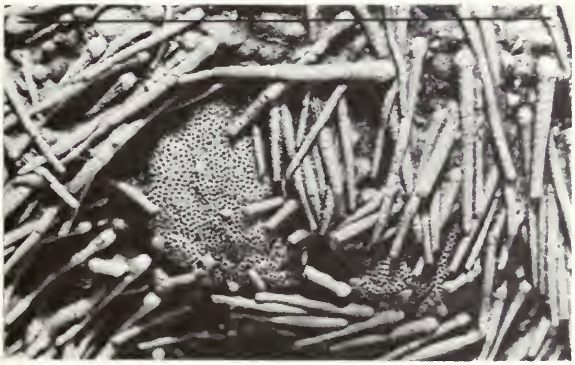

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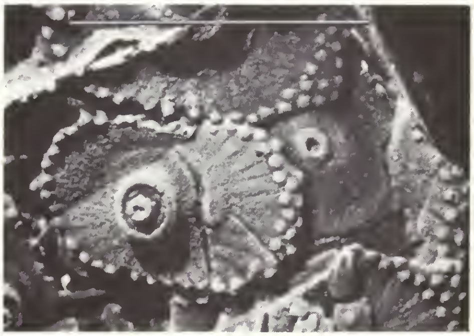

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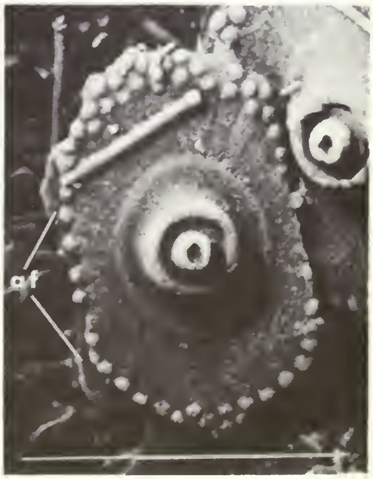

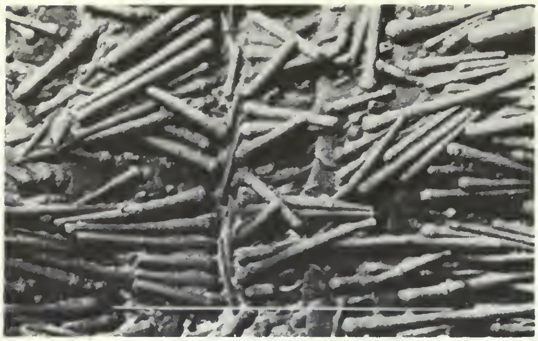
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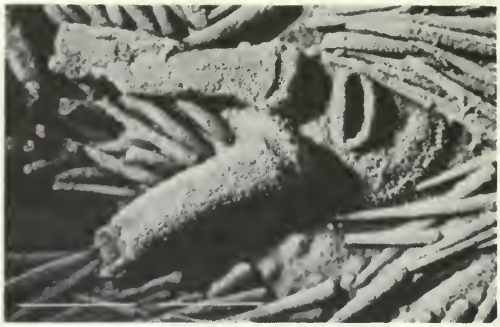
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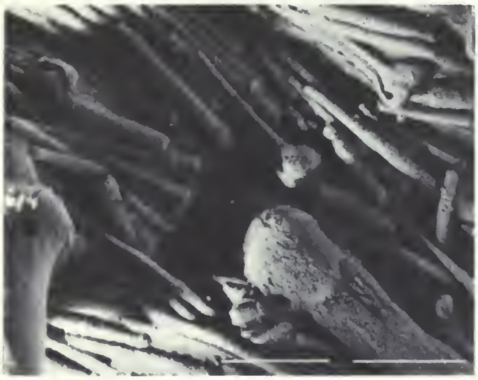
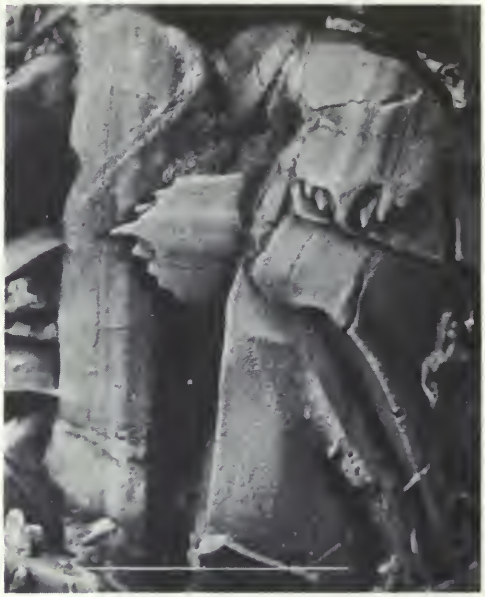

14a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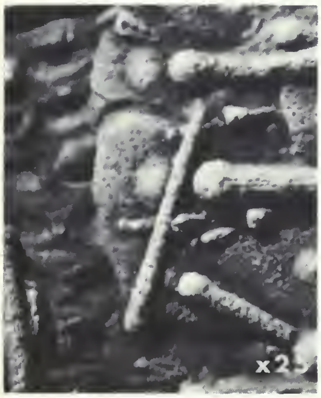
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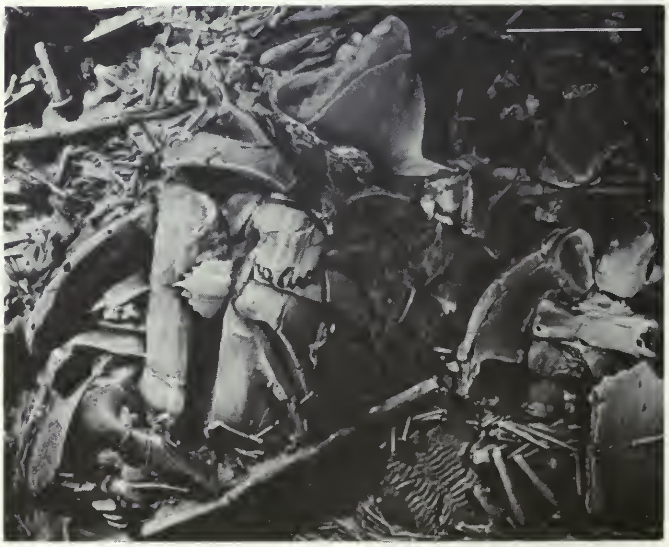
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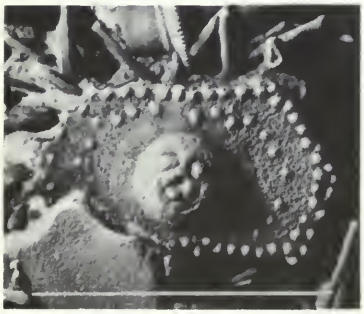

15a

The edge of the wing is gently, convexly curved to a level just below the deepest part of the retractor muscle scar. The edge then steepens its angle to almost vertical down to the tip of the demipyramid. The edge of the wing forms a thin wall for the retractor muscle scar, from the epiphyseal suture to the start of the nearly vertical part.

The surface of the wing has many curved ridges for interpyramidal muscles. They extend from the outer edge of the wing to the innermost edge where they give rise to faint serrations. The ridges are curved, being concave towards the epiphysis. The wing is almost triangular in outline, with an irregular epiphyseal suture, a convex outer edge to the wing, and a convex inner edge which meets the dental slide at right angles. The inner edge of the wing is here produced into a flange as part of the slide, and continues to the top of the demipyramid. The angle between the wing and the outside of the demipyramid is about 70°.

Close to the pyramidal suture there is a thin groove from the foramen magnum to the bottom of the demipyramid. Farther away from the suture is a broad, parallel-sided, gently convex portion, which also forms the other wall of the retractor muscle scar. The outermost tip of the demipyramid is straight. The inner surface of the demipyramid is concave across the width and down the length. The dental slide is a smooth, parallel-sided structure, raised above the area adjacent to the pyramidal suture. The lower end of the slide is straight, and the upper end sharply curved and undercut, and does not reach the margin of the foramen magnum. The area adjacent to the pyramidal suture tapers very gently from the foramen magnum to the top of the demipyramid. It is smooth, and partly represented on the outside of the demipyramid by the raised portion running from the foramen magnum to the tip. The remainder of the inner surface of the demipyramid is broad and tapers towards the prong.

The top surface of the demipyramid is sutured to the epiphysis. The margin of the surface is smooth and narrow around the prong, but widens to about three times the width a short way from the inner margin along the interpyramidal side. The wider part also has several very small pits in its surface. There is a narrow shelf from the outer edge to the inner edge partly formed by the smooth expansion of the margin and partly by a deeply pitted area. The vertical surface of the prong is heavily tuberculated and has several pits sunk vertically into the surface. The tuberculations are elongated and have vertical long axes.

b, Epiphyses (Fig. 17b). There are four epiphyses visible on the holotype, and three on paratype E.76887. The suture surface of the epiphysis with the demipyramid has heavy tuberculations which correspond to depressions in the surface of the demipyramid. The outer surface of each epiphysis is smooth. There is a flattened inner tubercle on the horizontal surface at the inner end of the epiphysis, and a bilobed, kidney-shaped outer tubercle directly behind it. On the interpyramidal surface of the epiphysis, extending from the outer margin to just over half way along the epiphysis, is a glenoid cavity. It is a concave, triangular depression, wider at the outer end, tapered beneath the bilobed tubercle.

c, Teeth (Fig. 16a, 16b). There are five teeth present on the holotype, two of which are almost *in situ* within the pyramids. There is only one tooth on paratype E.76887 and none on the rolled-up paratype E.76889. Each tooth is long and wide and is gently curved across the width (convex to the outside) and strongly curved along the length (convex to the outside) to fit the curvature of the dental slide.

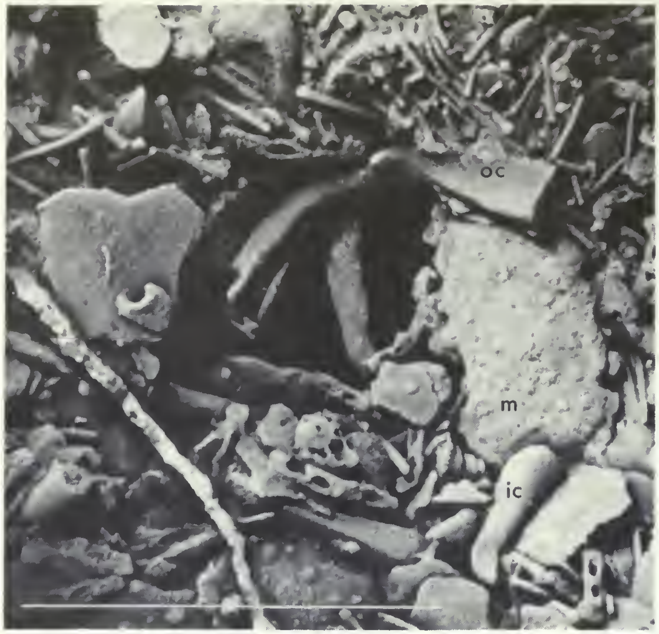
The teeth are longitudinally striated and grooved. Down the middle of the outside of the

Fig. 13 Part of ambulacrum III of the holotype E.76888 close to the madreporite, showing secondary radioles, miliary radioles, and the smaller pedicellariae.

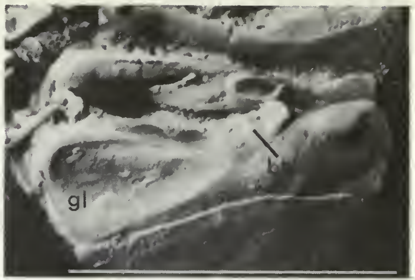
Fig. 14 Holotype E.76888. a, large pedicellariae amongst primary and secondary radioles of the adapical surface. b, small pedicellariae, miliary and secondary radioles, along ambulacrum III. The tubercles and stems of the pedicellariae can be seen lying close together.

Fig. 15 Holotype E.76888. a, unusual adoral interambulacral plate, showing a trilobed mamelon. b, unusual adapical interambulacral plate with two primary radioles.

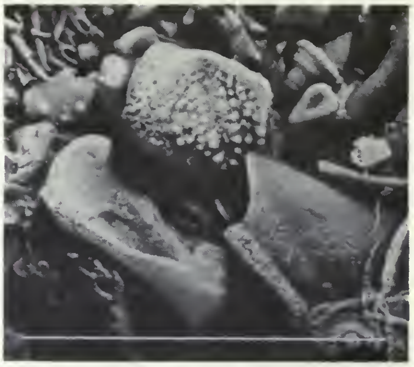
Fig. 16 Holotype E.76888. a, the broken Aristotle's lantern, showing demipyramids, epiphyses, rotulae, and teeth. Also present are several peristomial plates. b, detail of a, showing teeth with serrated tips.



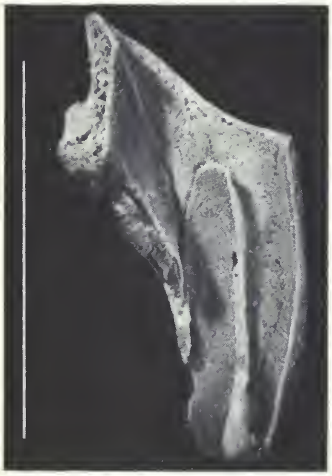
17a



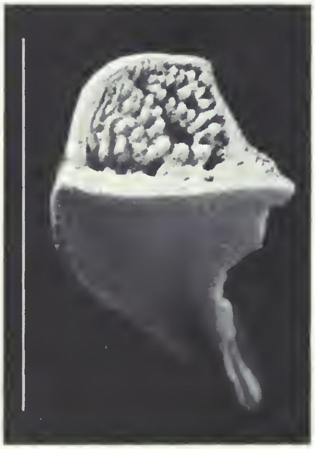
16c



17b



18a



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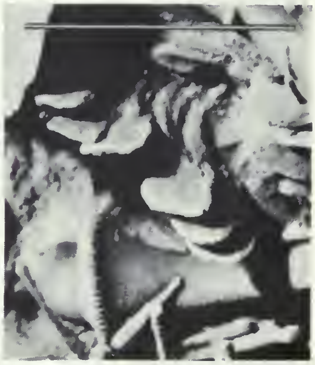
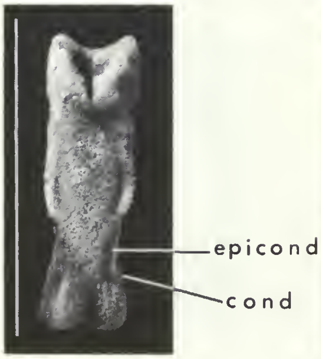


16d

19a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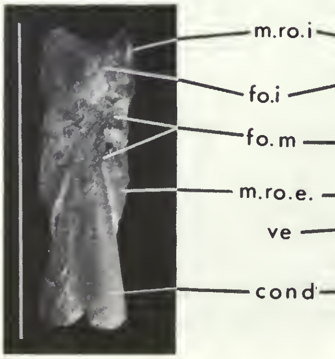
19b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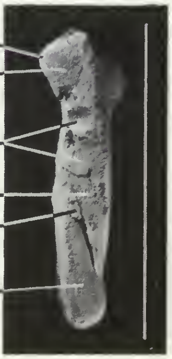

tooth is a broad double ridge corresponding to the smooth areas adjacent to the interpyramidal sutures on the insides of the demipyramids. The dental slide corresponds to the grooved portions on either side of the central double-ridged part of the tooth.

The tip of each tooth is serrated, with a single large median serration, and three smaller serrations either side of it. Each point of each serration is in a direct line with a groove on the tooth. The sides of the median serration overlap the proximal ends of one and a half of the lateral serrations each side of the tooth. If the serrations are ignored, a semicircular outline would be formed and not a half ellipse or a V shape.

The innermost ends of the teeth are not visible in the specimens as they are hidden by fragments of the test.

d, Rotulae (Figs 16a, 19a–c). There are three rotulae visible in the holotype, one in paratype E.76887, and a complete isolated rotula, E.76900 (Figs 19a–c). Only one rotula is close to its normal position, and this is in interambulacrum 3 of the holotype (see Fig. 16a), lying next to a jaw. Other rotulae have been completely separated from their jaws.

The rotulae of the specimens are the same length as the epiphyses. Each one is a sturdy, bilaterally symmetrical structure. The single isolated rotula (E.76900) is 9·9 mm long and 2·5 mm at its widest point, a ratio of almost 4 : 1. The upper surface is smooth, narrow towards the outer end at the epicondyles, wide from the centre to the inner end. The outer end is bilobed, forming condyles which articulate with the glenoid cavity. The inner end has a thick semicircular wall around a deep conical pit, open at the innermost end. The wall has a steep, deep, narrow groove from the top of the wall to the depth of the pit.

On the lower surface, the condyles taper beneath the upper surface, and also towards the two-part median fossa. There is a deep groove either side of the rotula, extending from the epicondyle of each condyle to the median fossae. The median fossa of each side has a large triangular facet and a smaller triangular facet separated from each other by a low ridge. The outer part of the two-part fossa has a raised rim at the outermost end.

The inner fossa of each side is situated on a downwards-pointing projection of the innermost end of the rotula. It takes the shape of a quarter circle. At the uppermost edge, a very low ridge separates the inner fossa from the interior rotula muscle scar, which is elongate from the edge of the inner end to a position just beneath the semicircular wall of the upper surface.

The sides of the rotula, apart from the condyles, slope towards the centre of the underside and join in a short flat ridge from the inner end of the condyle to the innermost end of the rotula. The external rotular muscle scar is present on the side of the rotula, at the outer end of the median fossa.

e, Compasses. There are four fragments of compass present in paratype E.76887 – two inner portions and two outer portions (Fig. 17a, 17b).

Each inner portion has a triangular cross-section and a hooked inner end. The upper

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Fig. 16 Holotype E.76888. c, epiphysis and rotula. The epiphysis is still *in situ* on its demipyramid, and shows the glenoid cavity (gl) and the bilobed tubercle (bt). d, the peristomial plates.

Fig. 17 Paratype E.76887. a, the outer portion of a compass (oc) showing the two long spikes and short lateral spikes. The madreporite (m) and an inner portion of compass (ic) are also visible. b, part of the inner contact surface of an epiphysis, showing the tuberculation. Also visible is the demipyramid belonging to the epiphysis and part of another epiphysis. A part of an inner portion of a compass is visible just to the right of the tuberculate epiphysis, and shows the triangular pit in its end.

Fig. 18 Demipyramid E.76899. a, the inner surface showing the dental slide. b, the upper surface showing the heavily tuberculated and deep-pitted demipyramid–epiphyseal contact surface.

Fig. 19 Rotula E.76900. a, upper surface. b, lower surface. c, side view. Abbreviations: cond = condyle; epicond = epicondyle; fo.i = inner fossa; fo.m = median fossa; m.ro.e = exterior rotula muscle-scar; ve = vestigial; m.ro.i = interior rotula muscle-scar. (Terminology of Märkel, 1979.)

surface is narrow, and slopes steeply over the sides, then curves beneath to form the triangle. The hook is down-curved from the upper surface and ends in a sharp point. On its lower surface there are two facets which meet in the centre in a blade. The non-hooked end is broader, and has a shallow triangular pit in its cross section. One of the inner portions appears to be complete (Fig. 17a). It has its hooked end on the adapical surface, and its broad end on the adoral surface, having been forced through the test *post mortem*. The other inner portion, on the adapical surface, is slightly damaged on its broad end.

The outer portion of the compass has a triangular cross-section on its inner end, with a shallow triangular pit, similar to the pit in the end of the inner portion of the compass (Fig. 17a). The triangular part flattens out towards the centre of the length of the outer portion. Two short lateral spikes are present, pointing towards, and form the attachments for the intercompass muscles. Farther towards the outermost end there are two long, thin, curved prongs. The triangular part of the outer compass is straight, but at the flattened area the portion begins to curve downwards and becomes steeper along the prongs. The angle between the prongs is about 70°, but because of its position within the test, it is not possible to measure this angle accurately. The length of the outer part of the compass without the prongs is 5 mm; length of the prongs is 4 mm. The length of the inner part of the compass is 3·6 mm. There is one complete outer portion of a compass and one incomplete portion which has lost its prongs.

RADIOLES (Figs 4, 6, 8, 11, 13, 14b). (1). Primary interambulacral radioles (Fig. 4). These are long and slender. Each radiole is approximately triangular in cross-section for most of its length, with convexly curved sides. Nearer to the milled ring the section is circular. Along the length of the shaft there are two rows of spinules, one row at each angle of the base of the triangle.

The holotype has several primary radioles which are in close contact with their tubercles. The lateral spinules are present on the adoral surface of the radiole and point towards the tip

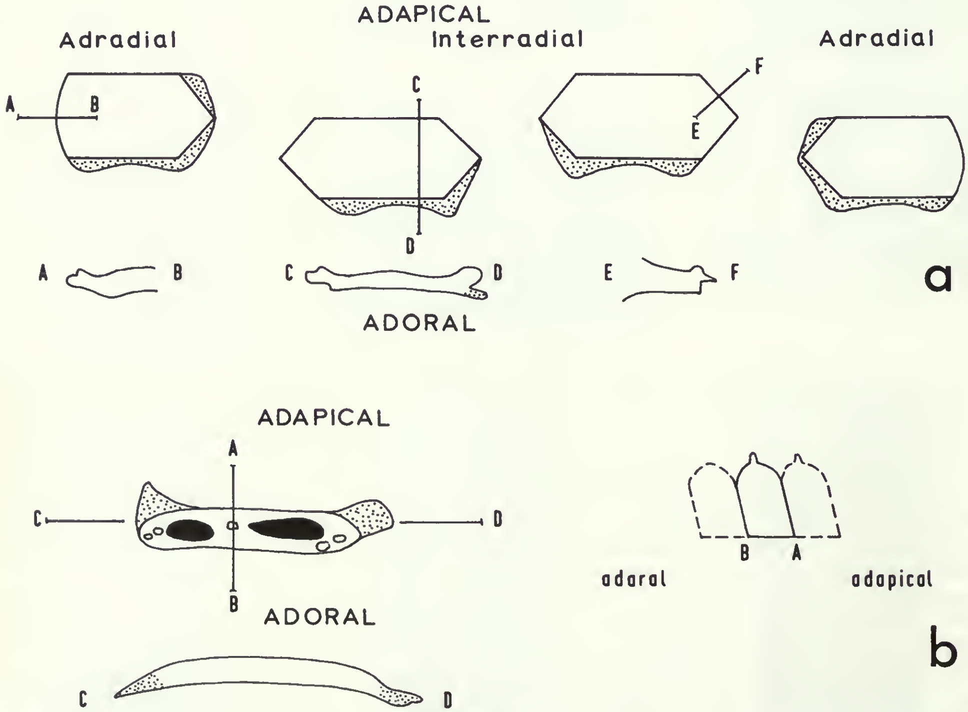

Fig. 20 Diagrams to show the positions of flanges (dotted) on (a) interambulacral and (b) ambulacral plates. Sketch sections show positions of flanges and facets.

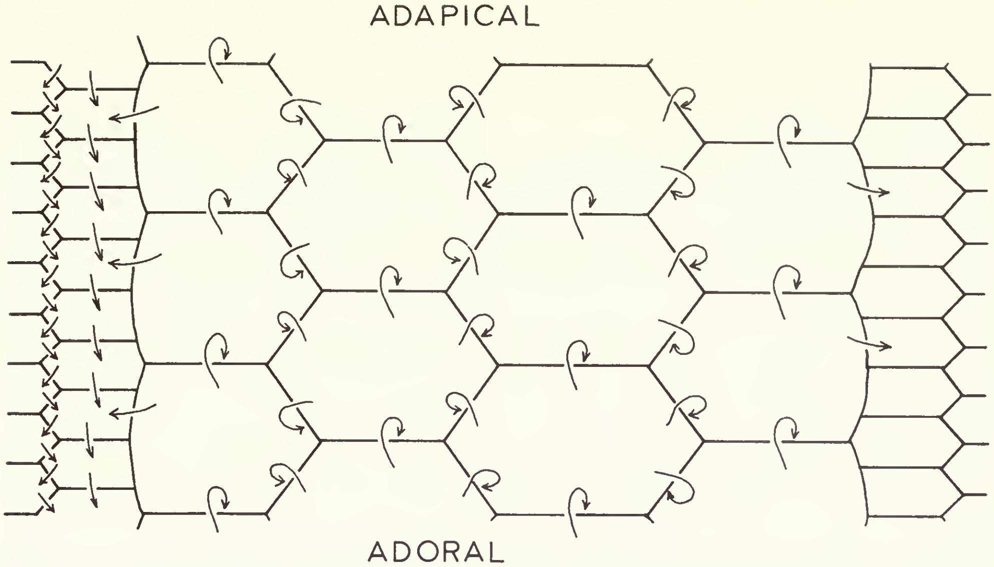

Fig. 21 Diagram to show directions of translation and directions of hinging when meridional muscle contracted. Gently curved arrows indicate direction of translation: reflexed arrows indicate direction of rotation.

of the radiole. The spinules may develop on opposite sides to each other, or they may develop alternately – there appears to be no constant pattern. Both arrangements do not, however, occur on the same radiole.

The shaft tapers towards the tip, and expands asymmetrically towards the milled ring, so that the shaft has its axis nearer to the adoral edge of the ring. The shaft has additional ornament of very fine longitudinal striations which increase in width over the collar before flaring out into the milled ring. The milled ring is tilted so that the adoral side is towards the tip of the shaft, and the adapical side is towards the tubercle. The striations forming the ridges of the milled ring continue to the underside, then stop at a raised rim. The rim is slightly concave where its adapical side joins the smooth base, and slightly convex on the adoral side. The deep acetabulum has a diameter about half that of the milled ring. It is centrally placed within the ring.

One of the primary radioles of the holotype is at least 51·5 mm long, but lacks the extreme tip. Some radioles have been crushed at the distal ends of their shafts in such a manner as to suggest hollow interiors. The paratype E.76889 has a few proximal ends of radioles remaining in contact with the test. These show hollow interiors near to the milled ring. Some radioles are slightly curved along their length, concave on their adapical sides. These are present mostly on the adapical surface of the holotype. The most adapical radioles are very much smaller than those at the ambitus.

(2) Secondary radioles (Figs 8, 13). These include the scrobicular radioles and the primary ambulacral radioles. All are small, about 6 mm long when complete, narrow, slender and solid. The shaft has ornament consisting of longitudinal striations somewhat coarser than the longitudinal striations of the primary interambulacral radioles. Each radiole has a thickening towards the proximal end which forms a milled ring. The base is smooth, convex and short, giving a bulbous appearance. The acetabulum is small.

The secondary radioles belong to the scrobicular tubercles, and to any other tubercles of this size and type which are not of the scrobicule. They are also attached to the tubercles of the ambulacra – the marginal tubercles and the tubercles of the adradial margins.

The secondary radioles of the holotype (see Figs 8, 13) are almost all present on the adapical surface of the test and the ambitus, but have been almost completely removed or disrupted on the adoral surface. The radioles are almost *in situ* but have been laid flat upon the test. The secondary radioles of paratype E.76889 (Fig. 6) are close to their tubercles and occur in parallel bunches.

(3) Miliary radioles (Figs 13, 14b). These are very small – between about 1·8 mm and 3 mm long. In other respects they resemble the secondary radioles. Mostly they are preserved on the adapical surface of the holotype. They belong to the smallest tubercles to be found distributed randomly over the interambulacra, and also to the inner tubercles of the ambulacra. The miliary radioles of the ambulacra lie parallel to the perradial sutures on the holotype.

The secondary and miliary radioles are also present on paratype E.76887, where they have been scattered randomly over the test on both surfaces. Paratype E.76889 displays only primary and secondary radioles.

Pedicellariae (Figs 13, 14a–b). There are two kinds of pedicellariae, both of them tridentate. The first is very large – almost as long as a secondary radiole, and the second kind is very small indeed, with valves barely as large as the 'bulb' of a secondary radiole. Both kinds are preserved only on the holotype.

The large pedicellariae (Fig. 14a) are present on the adapical and adoral side of the holotype, and on the adapical side are aligned parallel with the adjacent secondary radioles.

Each large pedicellaria consists of four parts – a stem and three valves. The stem is short, only about 2·8 mm long, and has a blunt proximal end, a cylindrical shaft and a short, tapered neck to join on to the proximal part of the valves. The valves each have a long, thin cylindrical part with longitudinal striations forming the ornament, and a triangular, rounded proximal part which is spoon-shaped and is about 0·5 m long, and has a dividing septum along the axis. The three valves fit together in a triple point which forms a flat surface for the stem to attach to. Where two valves are in contact at the proximal end there is a lens-shaped cavity. A complete valve is about 3·4 mm long. The complete pedicellaria is attached to a secondary tubercle. Some of the pedicellariae which are lying adjacent to secondary tubercles can be seen in interambulacra 2 and 3 of the holotype.

The smaller pedicellariae (Figs 13, 14b) are about 0·5 mm in total length; some are much smaller. They resemble the large pedicellariae in most respects except that the valves do not have the very long cylindrical distal part. Instead, the valves close a short way from the lens-shaped cavity. The stem joins a tubercle which is about a quarter of the size of a miliary tubercle. An example of a complete pedicellaria with its tubercle adjacent is present in interambulacrum 1. Others, with or without stems or tubercles, are present over the adapical face of the test, especially along the interambulacral margins of the adradial sutures.

Comparisons with other species of *Archaeocidaris*. *A. whatleyensis* differs from other species of the genus in that its primary radioles are approximately triangular in cross-section and bear only two rows of distally directed spinules. *A. triserrata* (American) and *A. triserialis* (European) are known only from their primary radioles which are triangular in section, but which have three rows of spinules. *A. triplex* (American) is known from primary radioles and some interambulacral plates. It has radioles with triangular cross-section and three rows of spinules. The plates are imperfectly known. Other species have different cross-sections and ornament on their radioles. These differences are summarized by Jackson (1912 : 258–259).

A. wervekei, from Germany and Belgium, differs from *A. whatleyensis* in that the height of its interambulacral plates equals or exceeds their width, and they have strong radial plications from basal terraces to plate margins. The interambulacral plates of *A. whatleyensis* on the other hand have greater width than height, and the radial plications of the tubercles are much less marked than those of *A. wervekei*.

A. urii, from Britain, Ireland, Belgium and Germany, is relatively common. It has many distally directed spinules on its radioles in many rows. The scrobicular tubercles are not so densely packed as those of *A. whatleyensis*, which also has many other secondary tubercles outside the scrobicular circles. *A. urii* does not have these tubercles. It has a smaller basal terrace and stronger radial plications to each tubercle than does *A. whatleyensis*.

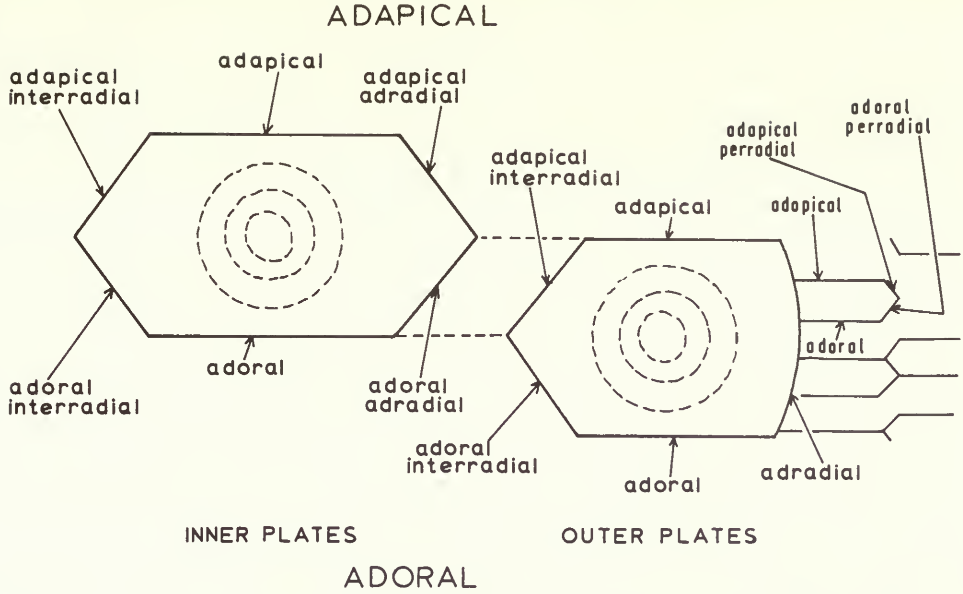
ADAPICAL
adapical interradial
adapical
adapical adradial
adoral interradial
adoral
adoral adradial
adapical interradial
adapical
adapical perradial
adoral perradial
adapical
adoral
adoral interradial
adoral
adradial
INNER PLATES
OUTER PLATES
ADORAL

Fig. 22 Terminology of the margins and sutures of interambulacral and ambulacral plates.

A. nerei, from Belgium, has cylindrical radioles with very fine longitudinal striations. The interambulacral plates are more convex than those of *A. whatleyensis* and have far fewer secondary tubercles.

The known Aristotle's lanterns of *Archaeocidaris* are all very similar in appearance. They all have wide-angled pyramids with moderately deep foramina magna. Detailed information is mostly lacking. However, specimens of jaw fragments of *A. nerei* from the Tournaisian of Tournai, Belgium (see Jackson 1929) in the collections of the BM(NH) show similarities to the jaws of *A. whatleyensis*. The demipyramids of *A. nerei* have tuberculations on the pyramid–epiphyseal suture just as *A. whatleyensis* does. The arrangement is only slightly different, and this may be due to the much smaller size of the demipyramids of *A. nerei*, especially specimens from groups numbered 32846 and E.9328 in the BM(NH). The teeth of both species are serrated at their tips, but those of *A. nerei* are much more slender, and if the serrations were to be ignored the outline of the tips would be distinctly V-shaped and not semicircular as in *A. whatleyensis*. The median serration is raised above the lateral serrations and only overlaps the proximal end of one serration each side in *A. nerei*. Instead of a double-ridged central portion to each tooth, as in *A. whatleyensis*, there is a flattened V-shaped groove. Examples of these teeth have been examined in the BM(NH) from groups numbered E.9323 and E.9324.

Compasses are rarely found in Palaeozoic echinoids, but are previously known from *A. rossica*. The compasses of *A. rossica* do not have the very long prongs of the outer portion that are present in *A. whatleyensis*. Isolated outer portions of the compasses of undetermined Palaeozoic echinoids were reported by Hoare & Sturgeon (1976), and these also have short prongs. Hoare & Sturgeon also collected many isolated demipyramids which resemble those of *Archaeocidaris*, and which appear to have tuberculations on the upper surface where the epiphyses join, somewhat similar to those of *A. nerei* and *A. whatleyensis*. It is likely that other species of *Archaeocidaris* also have these tuberculations and pits, if only they could be found.

Discussion

The classification of the echinoids which is used by Fell (1966) in the *Treatise on*

Invertebrate Paleontology came before the rise of cladism. As a result the *Treatise* divides the Echinoidea into two groups – the Perischoechinoidea and the Euechinoidea. The Perischoechinoidea include all the Palaeozoic echinoids plus the Cidaroida, and the Euechinoidea includes all the remainder of the Echinoidea. In the light of Hennigian methodology this arrangement is unsatisfactory since, though the Euechinoidea are monophyletic, the Perischoechinoidea are paraphyletic (see Hennig 1969, 1981).

The basic concepts of Hennig no longer need explanation, but his ideas concerning the positioning of fossils in a classification are less well known. They depend on his concepts of the 'stem group' and what he called the '*group' (= crown group of Jefferies, 1979). These concepts are explained before we discuss how *Archaeocidaris* is related to other echinoids.

Suppose that two sister groups, 1 and 2, each contain several surviving member species. When fossils are considered, sister group 1 can be considered from two viewpoints.

The first is a narrower viewpoint comprising the latest common ancestral species of living members of group 1 and all descendants of that species living or extinct. This is the *crown group*. The second is a wider viewpoint comprising all descendants of the latest common ancestor of both groups 1 and 2, but minus all members of group 2. The wider viewpoint is the *total group* 1. If the crown group of group 1 is removed from total group 1 the remaining forms are called the *stem group* of group 1. The stem group is composed of extinct forms and is paraphyletic. It includes those species leading from the latest common ancestor of both groups 1 and 2 to the latest common ancestor of group 1 (the *stem line*) and also all descendants of that line except members of the crown group.

All surviving monophyletic groups with more than one species can be divided into stem groups and crown groups, but this is only useful if fossils are known. The real advantage of the stem group concept is that fossil species can be assigned to a stem group merely by the presence or absence of synapomorphies. To *prove* that a fossil belongs to a stem line of descent, on the other hand, requires complete stratigraphical data for all the species involved.

The stem group can be divided further by noting how closely related its component species are to the members of the crown group. The synapomorphies characterizing a member of an extant monophyletic group have not evolved all at once but by stages, being present in some members of the stem group and primitively absent in others. This enables the stem group to be split into *intermediate categories* (*Zwischenkategorien* of Hennig). The smallest unit of an intermediate category is the *plesion* (Patterson & Rosen 1977), which comprises all those members of a stem group which are equally related to the crown group. The plesion will possess a synapomorphy in common with the crown group which more primitive plesions lack, and will lack a synapomorphy which more advanced plesions have. This is sometimes confused by a character being secondarily lost.

The classification of the echinoids can be expressed in terms of sister groups and of stem and crown groups, and a cladogram constructed (Fig. 23). This shows that the presumed ancestor had the following characters: four or more columns of plates per interambulacrum; a flexible test; hollow primary interambulacral radioles; perforate primary interambulacral tubercles; a hinge-jointed lantern; shallow-angled pyramids; a fairly deep, U-shaped foramen magnum; a pyramid–epiphyseal suture with pits and tuberculations; and peristomial plates with two columns per ambulacrum and many columns of interradial plates.

The synapomorphies of stem and crown echinoids are as follows (numbers refer to Fig. 23):

1. Gain of triangular section for primary interambulacral radioles.
2. Gain of rigid interambulacra.
3. Gain of rigid test.
4. Gain of solid radioles.
5. Gain of apophyses in perignathic girdle.
6. Gain of steep-angled pyramids.
7. Gain of crenulate tubercles.
8. Gain of smooth-surfaced pyramid–epiphyseal sutures with deep pits in demipyramids.

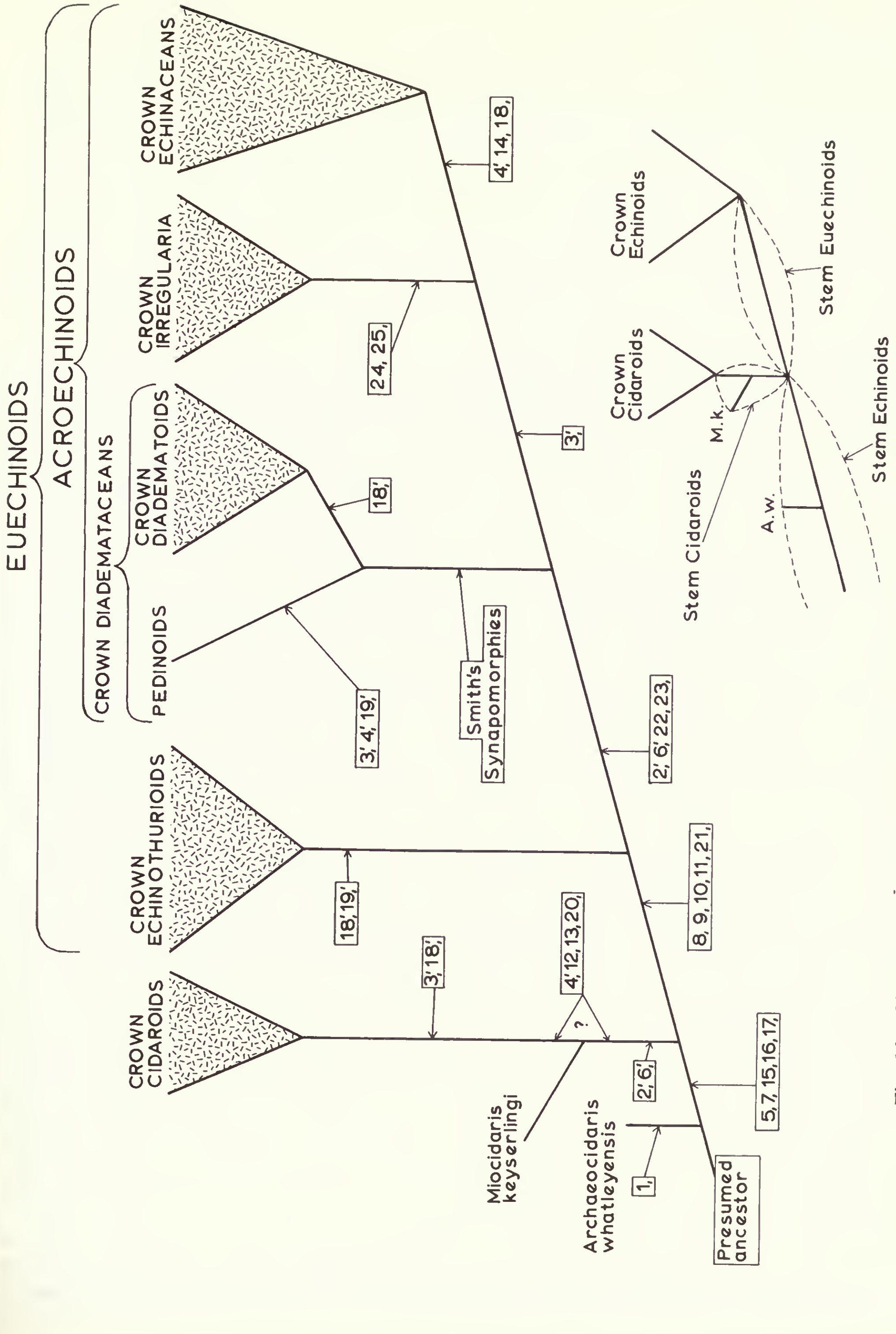
EUECHINOIDS
ACROECHINOIDS
CROWN DIADEMATACEANS
CROWN CIDAROIDS
CROWN ECHINOTHURIOIDS
PEDINOIDS
CROWN DIADEMATOIDS
CROWN IRREGULARIA
CROWN ECHINACEANS
Miocidaris keyserlingi
Archaeocidaris whatleyensis
Presumed ancestor
1,
2,′6,′
5,7,15,16,17,
?
4,′12,13,20,
3,′18,′
8,9,10,11,21,
18,′19,′
2,′6,′22,23,
3,′4,′19,′
Smith's Synapomorphies
18,′
3,′
24,25,
4,′14,18,
Stem Cidaroids
M.k.
A.w.
Crown Cidaroids
Crown Echinoids
Stem Echinoids
Stem Euechinoids

Fig. 23 Cladogram showing the principal synapomorphies of the stem echinoids, the cidaroids and the euechinoids; see text for detailed explanation. When a feature evolves more than once we have inserted a ‘′’, e.g. 3′, whenever it appears.

9. Gain of auricles.
10. Gain of external gills and gill slits.
11. Gain of compound ambulacral plates.
12. Gain of socket-joint lantern.
13. Gain of shallow foramen magnum.
14. Gain of keeled teeth.
15. Loss of two columns of plates per interambulacrum.
16. Loss of tuberculation of pyramid–epiphyseal suture.
17. Loss of all interradial buccal plates except for one column.
18. Loss of flanges on plates.
19. Loss of crenulations on tubercles.
20. Loss of pits in pyramid–epiphyseal suture.
21. Loss of interradial buccal plates.
22. Loss of ambulacral buccal plates except five pairs at the mouth.
23. Loss of Stewart's organs.
24. Loss of periproct from apical disc by migration adorally.
25. Gain of bilateral symmetry.

The cladogram shows the Archaeocidaridae as part of the stem group of the Echinoidea. *Miocidaris keyserlingi* belongs to the stem group of the cidaroids. The echinothurioids are the primitive sister group to the acroechinoids, i.e. all the remaining euechinoids (see Smith 1981). The diademataceans (*sensu* Smith, 1981) comprise the pedinoids plus the diadematoids, with the pedinoids as the sister group to the diadematoids. The echinaceans include all the remaining echinoids except the Irregularia (*sensu* Smith, 1981). The echinothurioids plus acroechinoids make up the crown Euechinoidea. The *Treatise* taxon Perischoechinoidea, which groups together all Palaeozoic echinoids plus the Cidaroida, must be rejected because it is paraphyletic and is not a stem group.

The cladogram suggests that the presumed ancestor in Fig. 23 had features which are still represented in living euechinoids. But *Archaeocidaris* possesses at least one character more primitive than any possessed by crown echinoids, i.e. four columns of plates per interambulacrum. It also possesses features which were probably shared with the latest common ancestor of living echinoids, i.e. the first crown echinoid. These features include: a flexible test, perhaps hollow primary radioles, hinge joints in the lantern, shallow-angled pyramids, fairly deep, U-shaped foramina magna, pyramid–epiphyseal suture with pits and tuberculations, perforate tubercles, and many rows of buccal plates both ambulacral and interradial. Descendants of the first crown echinoids may retain some of these primitive characters, but have lost others.

Sarasin & Sarasin (1887–8), in their description of the living echinothurioid *Phormosoma*, described the method by which the ambulacral plates imbricate over each other. This happens by means of the meridionial muscles which are attached to the aboral parts of the auricles at one end and to the ocular plates at the other, and pass along the inner adradial edge of the ambulacral plates, and also the peristomial plates. By contracting these muscles, the ambulacra are shortened, causing the ambulacral plates to imbricate adorally, and at the same time increasing the curvature of the test by causing the interambulacra to bend at the plate margins. It seems likely that similar muscles were present along the corresponding ambulacral margins of *Archaeocidaris*, with comparable effects when they contracted. However, the meridional muscles were not found in diadematids when these were examined by the Sarasins. At the adradial margins of *Archaeocidaris* the interambulacra imbricated perradially over the ambulacra. The mesenteries of living diadematids, though apparently without muscles, are arranged exactly like the muscle-bearing mesenteries of *Phormosoma*, which suggests that such arrangement of mesenteries is primitive for crown euechinoids and could well have existed in *Archaeocidaris* also.

Flexible tests were present in stem echinoids such as the Archaeocidarids, stem cidaroids and in primitive crown echinoids. Some species placed traditionally in the genus *Miocidaris* had tests which were either wholly flexible or only partly so. Those which had wholly flexible tests have ambulacral plates of a similar construction to those of *Archaeocidaris*

(Kier 1965, 1968). They are very like an *Archaeocidaris* but with only two columns of plates per interambulacrum (e.g. *Miocidaris connorsi* Kier, 1965). The species of *Miocidaris* with entirely flexible tests are either advanced stem echinoids, or are primitive stem euechinoids or stem cidaroids. The species with rigid interambulacra such as *M. keyserlingi* are probably stem cidaroids. Crown cidaroids have rigid tests. *Miocidaris* as defined in the *Treatise* is paraphyletic.

Some living euechinoids have flexible tests. Echinothurioids such as *Phormosoma* are wholly flexible by means of a tough flexible membrane between the plates which allows flexing of the test and holds the plates together. There are no flanges on its interambulacral plates. If the flexibility of the tests of echinothurioids is homologous with that of *Archaeocidaris*, they form the primitive sister group to all other living euechinoids. These others have been called the Acroechinoidea by Smith (1981) and their tests are more rigid than those of echinothurioids, though diadematoids retain slight flexibility. The rigid test of acroechinoids was probably acquired independently of that of cidaroids.

Stem echinoids such as *Archaeocidaris* did not possess a perignathic girdle for the attachment of the lantern muscles. These muscles were presumably attached directly to the interambulacral plates of the peristome. Stem cidaroids, however, had a perignathic girdle, formed by the apophyses. Crown euechinoids have apophyses and auricles. Stem echinoids and all cidaroids have no gill slits, but these are present in the euechinoids.

Peristomial plates extend from the border of the peristome to the mouth and may consist of ambulacral plates, interradial plates, and in some euechinoids some plates of uncertain origin. In *Archaeocidaris* the plates of the peristome consist of several columns of imbricating perforate ambulacral plates, and several columns of imbricating interradial plates. This is probably the case for all stem echinoids. Stem and crown cidaroids have two columns of ambulacral peristomial plates extending from each ambulacrum to the mouth. There is only one column of interradial plates extending from the peristomial border to the mouth of crown cidaroids; the evidence for interradial plates in stem cidaroids is lacking. The echinothurioid *Phormosoma* has two columns of large ambulacral peristomial plates extending from each ambulacrum, but it has no interradial plates. A syntype of the type species of *Echinothuria* (BM(NH) 40240)) has part of a double column of ambulacral peristomial plates preserved, but has no interradial plates visible. It is most likely that *Echinothuria* resembled *Phormosoma* in this respect. The diademataceans, as part of the advanced sister group to the echinothurioids, have only five pairs of peristomial plates in a ring around the mouth. Thus, the primitive condition of the peristomial plating seems to be that of many columns of ambulacral and interradial plates as found in *Archaeocidaris*. From this came the double columns of ambulacral plates plus single rows of interradial plates as in the cidaroids, and the double columns of ambulacral plates only, as in *Phormosoma*. From a *Phormosoma*-like condition arose the situation with just five pairs of ambulacral oral plates situated at the edge of the mouth, as in *Diadema*.

Some features of the Aristotle's lantern have also evolved. The pyramids of *Archaeocidaris* are low-angled and wide, each with a fairly deep and broad foramen magnum. The demipyramid–epiphyseal suture is very tuberculate, with shallow pits in the upper surface of the demipyramid. Crown cidaroids have steep-angled pyramids, each with a very shallow foramen magnum, and smooth demipyramid–epiphyseal sutures with no tuberculations or pits. *Echinothuria* has pyramids which are steeper-angled, but its living relative *Phormosoma* has shallow-angled pyramids reminiscent of *Archaeocidaris*. However, *Phormosoma* does not have the complex tuberculation and shallow pits on the demipyramid–epiphyseal suture. Instead these surfaces are smooth, with deep pits in the demipyramid. If the shallow pits of *Archaeocidaris* are homologous with the deep pits in the demipyramids of the crown euechinoids, then this feature will be a primitive character as compared with the smooth surface without pits of the cidaroids. The fairly deep U-shaped foramen magnum of *Archaeocidaris* is primitive when compared with the shallow foramen magnum of cidaroids, and the deep V-shaped foramen magnum of the euechinoids.

Märkel (1979) described the two different types of joint between the epiphyses and the rotulae in living cidaroids and non-cidaroids. He calls the joints 'socket joints' in the cidaroids, using *Eucidaris tribuloides* as an example, and 'hinge joints' in non-cidaroids. Cidaroids have hemispherical condyles on the rotulae, with corresponding hemispherical glenoid cavities in the epiphyses to form ball-and-socket joints. The non-cidaroid joints have elongate condyles and glenoid cavities to form a hinge. *Archaeocidaris*, however, has the hinge-joint type, unlike living cidaroids and exactly like living euechinoids. The hinge joint is therefore probably a primitive character already present in the stem echinoids, present in the first crown echinoid and retained in living non-cidaroids, whereas the socket joint is an advanced cidaroid character.

The primary radioles of *A. whatleyensis*, some other species of *Archaeocidaris*, echinothurioids, diadematoids, early pedinoids (*sensu* Smith, 1981), atelostomes and gnathostomes are hollow for all or most of their lengths. Other species of *Archaeocidaris*, *Miocidaris*, crown cidaroids and remaining acroechinoids have solid primary radioles. If hollow radioles are a primitive character then *Archaeocidaris* contains two groups. The group with hollow radioles would be closer to the primitive condition and would be paraphyletic, whilst the group with solid radioles is probably a monophyletic group showing parallelism with the cidaroids and also some acroechinoids. If the radioles of *M. connorsi* are hollow, as suggested by the photograph in Kier (1965), this supports the idea that hollow radioles are primitive for crown echinoids.

The ambulacral plates of *Archaeocidaris* and *Miocidaris* are not compound but form two simple columns in each ambulacrum. Some crown cidaroids show a simple kind of compounding (probably better called pseudocompounding), e.g. *Stereocidaris grandis*, *Paracidaris, Diplocidaris, Alpicidaris* and *Tetracidaris* (see Mortensen 1928 : 11–15). In these genera the marginal tubercle of one plate increases in size so that it sometimes displaces the marginal tubercle of adjacent plates, and sometimes the adjacent plates lack the tubercle. The enlarged tubercle only develops on its own plate. In *Diplocidaris* the pores are displaced alternately to give a double series of pore-pairs. This kind of compounding is probably a parallelism with that of the euechinoids. Diadematids have plate compounding in their typical triads, and *Echinothuria* and *Phormosoma* have a version of diadematid triad compounding sometimes similar to the 'arbacioid' type of compounding (see *Treatise*; Fell 1966 : 231).

The primary interambulacral tubercles of *Archaeocidaris* and the echinothurioids are perforate and non-crenulate, whilst those of *Miocidaris* (e.g. *M. keyserlingi*) are perforate and crenulate. Crown cidaroids may or may not have crenulate tubercles, but all have perforate tubercles except the Psychocidaridae (e.g. *Tylocidaris*) which have non-perforate tubercles. *Tylocidaris* bears traces of perforation in the most adapical interambulacral tubercles, indicating that loss of perforation in this genus is secondary. Diadematids have perforate tubercles and may or may not have crenulate tubercles.

Within the *Treatise* definition of the Miocidaridae there are some genera which have crenulate primary interambulacral tubercles, and others with non-crenulate tubercles. Crown cidaroids have genera with either crenulate or non-crenulate tubercles. The primitive condition for crown cidaroids was almost certainly with crenulate tubercles as in the stem cidaroid *M. keyserlingi*. On the other hand, the absence of crenulations in *Archaeocidaris* (and all other Palaeozoic echinoids) is most likely to be primitive. Either crenulations are primitive for crown echinoids, or they have evolved more than once. If they have evolved more than once then miocidarids with crenulate tubercles are probably stem cidaroids, and the crenulate tubercles of some acroechinoids evolved separately. If they have evolved once only and have been lost several times then 'miocidarids' with crenulate tubercles could be advanced stem echinoids, with some crown cidaroids, echinothurioids, and some euechinoids losing their crenulations. It is more parsimonious to suppose that crenulate tubercles evolved once and have been lost several times than to believe they evolved more than once.

Conclusions

A. whatleyensis, and *Archaeocidaris* in general, is shown to be a stem echinoid by the presence of four columns of plates in each interambulacrum. *A. whatleyensis* demonstrates that many features which have been seen as synapomorphies of euechinoids in fact existed already in the stem group of echinoids. These features of the euechinoids may therefore be considered to be probably primitive for crown echinoids as a whole. They include:

1. Upper surface of pyramids with pits.
2. Hinge joints in the Aristotle's lantern.
3. Shallow pyramid angles in the lantern, with broad, U-shaped foramina magna.
4. Perhaps hollow radioles.

Moreover, the flexibility of the test of *Archaeocidaris* is probably homologous with that of echinothurioids. The rigid test of acroechinoids has therefore probably been acquired independently of that of the cidaroids.

Crown cidaroids have some advanced characters which are unique to them, and which are represented in the euechinoids by more primitive characters. The advanced characters include:

1. Upper surface of pyramids smooth, without pits.
2. Socket joints in the lantern.
3. Shallow and small foramina magna, steep pyramid angles.

The rigid test of crown cidaroids has probably been acquired separately from that of the acroechinoids.

Acknowledgements

We would like to thank Dr R. P. S. Jefferies, BM(NH), and Dr A. B. Smith, University of Liverpool, for helpful discussions and suggestions during the progress of this paper, and Dr C. Forbes and staff of the Sedgwick Museum who made material available from their collections. Dr G. F. Elliott and Dr R. M. Owens also contributed discussions. Thanks are due to the BM(NH) Photographic Unit for some of the photographs, and to Mr R. P. Shaw for the donation of the paratype E.76887 to the National Collections. We would also like to thank the Archaeology Department of the University of Leicester for the use (by P.C.E.) of their air-abrasive machine for the initial preparation of the specimens.

P.C.E. would also like to acknowledge with thanks the assistance, in the form of accommodation and transport, of Mr & Mrs D. Ensom.

Finally, thanks are due to the Manager and staff of A.R.C. Whatley Quarry, Somerset, for access to the quarry, without which the specimens would have been lost.

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A possible non-calcified dasycladalean alga from the Carboniferous of England

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Synopsis

Dasycladophycus ensomi gen. et sp. nov. is described from the Lower Carboniferous of Somerset, England. It is interpreted as possibly a non-calcified dasycladalean alga.

Introduction

The little fossil described below, collected by Mr Paul Ensom, is from the Carboniferous of Somerset, England. It accompanies the echinoid *Archaeocidaris whatleyensis* Lewis & Ensom, described herein (p. 81). It shows as flattened, black, carbonaceous plant remains on the rock-surface. The structure is like that of a simple non-calcified dasycladalean; comparable algae are known from the Lower Palaeozoic and are still living. This is discussed in detail below, after the description of the alga.

Systematic

? Phylum **CHLOROPHYTA**

Order **DASYCLADALES**

Genus ***DASYCLADOPHYCUS*** nov.

DIAGNOSIS. Simple non-calcified alga showing central stem (? stem-cell) with regular verticils of four branches: each branch straight, slightly swollen, and dividing terminally into four very short branchlets. Holdfast and reproductive structures not seen; associated long whip-like strands possibly part of the plant.

TYPE SPECIES. *D. ensomi* sp. nov.; Lower Carboniferous.

Dasycladophycus ensomi sp. nov.

Fig. 1

DESCRIPTION. The plant is represented by relics of several individuals, all flattened black carbonaceous remains on the rock-surface. The best example shows as a thallus 14 mm long and 3 mm wide (in the flattened state), Fig. 1. From the central stem, about 0·5 mm wide, arise regular whorls or verticils of formerly radiating side-branches, the verticils regularly about 0·5 mm apart in succession. The side branches are about 1·5 mm long and 0·25 mm or less in diameter, swelling slightly from the junction with the central stem as in various known dasycladaleans. Terminally each shows four very short secondary branchlets. Because of the tangled, pressed preservation, it is difficult to evaluate the number of branches per verticil, but four seems probable.

On the rock-face there are long, thin, whip-like single carbonaceous strands, several times the length of the thallus. One or two appear to arise from a thallus, but this is not absolutely

Bull. Br. Mus. nat. Hist. (Geol.) **36** (2) : 105–107 Issued 28 October 1982

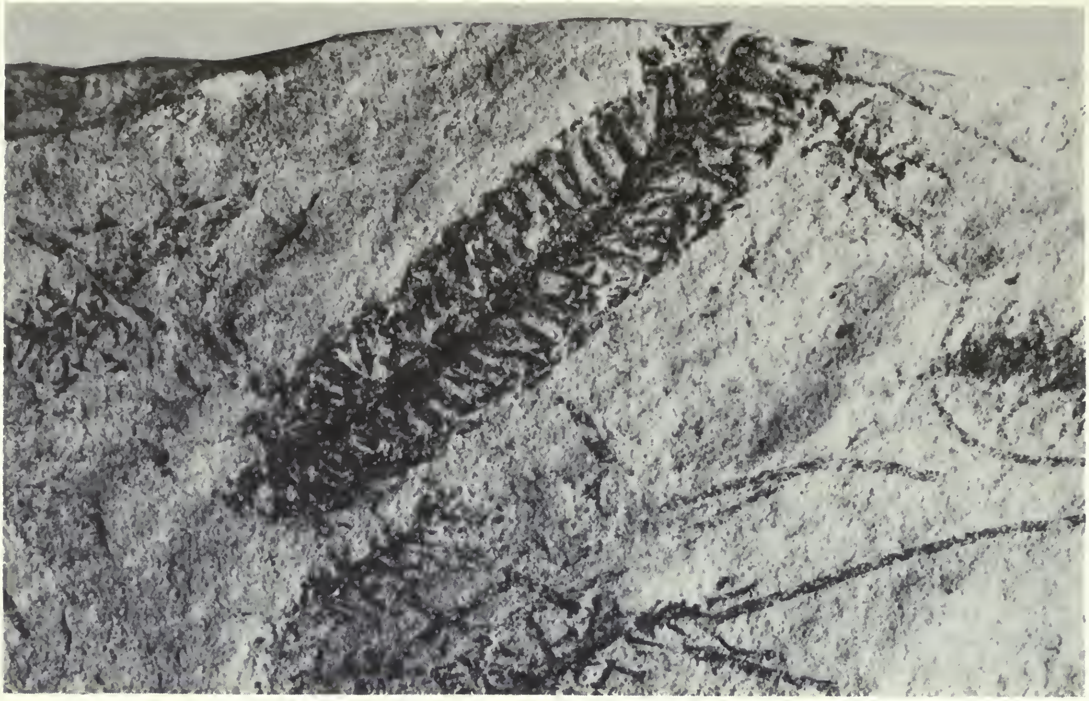

Fig. 1 *Dasycladophycus ensomi* gen. et sp. nov., thallus with associated long strands, **holotype** ×7. British Museum (Natural History), Department of Palaeontology, register number V.60786.

clear. They are in the same preservation and closely associated with the remains described above.

Holotype. British Museum (Natural History), Dept of Palaeontology, register number V.60786. From the Lower Carboniferous Clifton Down Limestone (Holkerian) of New Frome Quarry, Whatley, Somerset. Fig. 1.

Discussion. The morphology of this little plant is very much like that of a simple non-calcified dasycladalean. The non-calcified living *Batophora* shows side-branches with more complicated branching systems and bearing reproductive bodies. From the Ordovician, *Archaeobatophora* (Nitecki 1976) is surprisingly similar to *Batophora*, but does not show reproductive bodies. The Silurian *Inopinatella* (Elliott 1971) is similarly preserved and more like *Dasycladophycus* in the simplicity of its branch-structure, though still differing; it was interpreted by me as probably a simple dasycladalean, and compared with abnormal juveniles of a living genus in their pre-calcified stage. The very limited evidence offered by the *Dasycladophycus* fits with a dasycladalean interpretation.

The long whip-like strands could possible be remains of another alga, formerly growing on the same sea-floor and now associated in death. But they appear to be very much part of the remains preserved, even though their junctions with the thalli described are not certain. Comparison with accounts of the living *Caulerpa* (not a dasycladalean), where a system of long prostrate 'runners' throw up branched vegetative growths, convinced me that the Carboniferous fossil remains were not referable to this kind of alga. If the fossils are in fact dasycladalean then it is possible that several long single strands arose from the holdfast of a single *Dasycladophycus* thallus, which itself could have been eventually the fertile part of the whole plant. But this does not occur in any other Dasycladaleans to my knowledge and must remain a speculation.

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Nanjinoporella, a new Permian dasyclad (calcareous alga) from Nanjing, China

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Synopsis

A new Lower Permian dasycladalean alga, *Nanjinoporella pagoda* gen. et sp. nov., is described from China. It may be closely related to another Asiatic species, *Epimastopora malaysiana* Elliott, and shows an important advance on the incipient annulation of this latter species. Some notes on dasycladalean annulation generally are appended.

Introduction

The material described in this paper was sent to Mu Xinan by Mr Min Qing-kui; it was collected by him and his colleagues from the base of the Chihsia Formation of Lower Permian age (Artinskian/Leonardian) at Chihsia Shan hill, the type locality of the Formation, 25 km east of Nanjing.

Although the fossil alga is represented by only one specimen which was embedded in a piece of dark grey limestone, thanks to the skill of Mr Ji Cheng-dao, of the Rock Cutting Laboratory of Nanjing Institute of Geology and Palaeontology, several orientated sections have been prepared which reveal detailed information about the structure of the calcareous skeleton of the plant. Based on these thin sections, a new dasyclad genus *Nanjinoporella* has been recognized.

Conventional studies of calcareous algae are mostly based on random thin sections. The disadvantage of this method is that the reconstruction of the skeletal structures of the plant is always from different individuals, with the risk that individual sections from different species may be wrongly combined. Hence orientated sections from a single individual specimen are ideal. The preparation of such orientated sections is easier from isolated solid specimens which are available through natural weathering or by etching silicified samples in limestone, and for fossils embedded in matrix it is difficult but not impossible. The present study, describing *Nanjinoporella* and discussing the problem of its taxonomy and phylogeny, provides an example of this approach. Some notes are also given on the annulation structure in Dasycladaceae.

Systematic palaeontology

Family **DASYCLADACEAE** Kützing, 1843 orth. mut. Hauk, 1884

Genus *NANJINOPORELLA* nov.

Name. Referring to Nanjing, the capital of Jiangsu province, China.

Diagnosis. Near-cylindrical club-shaped dasyclad with large central stem and thin calcareous wall perforated by numerous close-set cylindrical pores, with slight constriction

Bull. Br. Mus. nat. Hist. (Geol.) **36** (2) : 109–116

Issued 28 October 1982

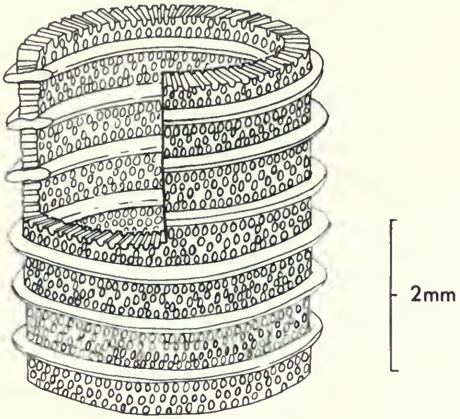


Fig. 1 Reconstruction of *Nanjinoporella pagoda* sp. nov., to show internal and external structure of calcareous wall (size of pores not in proportion).

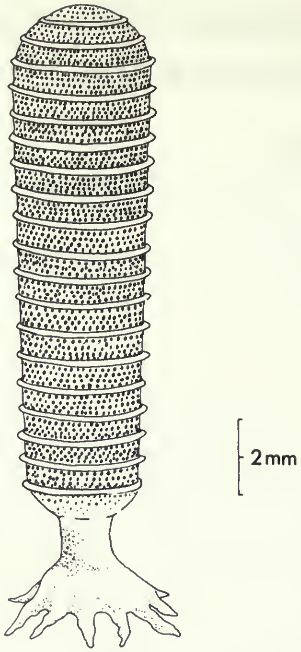


Fig. 2 Reconstruction of *Nanjinoporella pagoda* sp. nov., as in life.

at both ends. Pores show a trend to euspondyl arrangement and are separated at regular intervals by strongly developed outer and inner calcareous annulations (rings), dividing the pores into regular bands or zones.

TYPE SPECIES. *Nanjinoporella pagoda* sp. nov.

Nanjinoporella pagoda sp. nov.
Figs 1–6

NAME. The alga has the appearance of a pagoda.

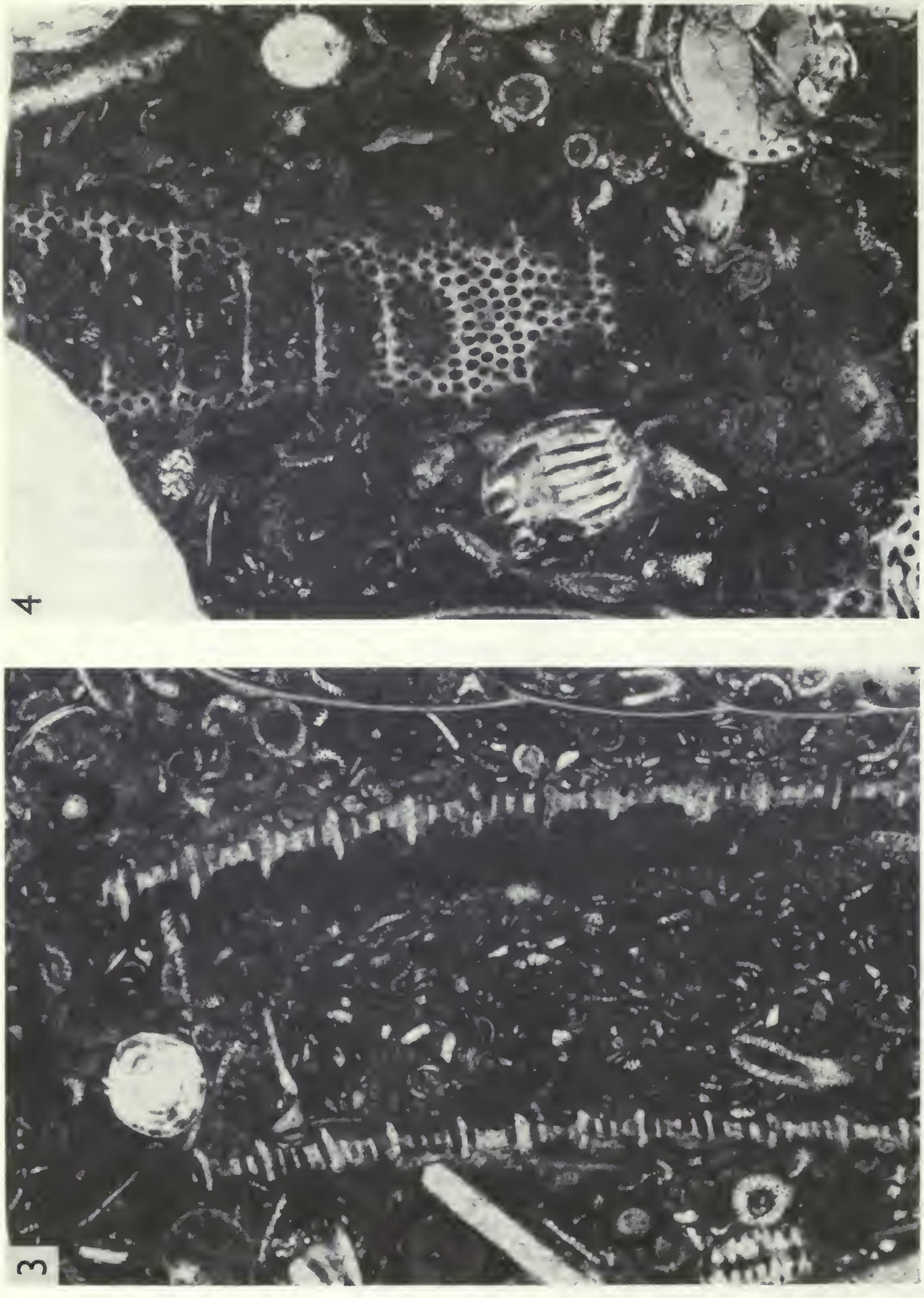
DESCRIPTION. The thallus is largely cylindrical in form and circular in cross section. The observed length (incomplete) is 10 mm and the former total length must have been considerably more. The outer diameter of the thallus increases from 3·63 mm proximally to 4·12 mm distally. Of two cross sections made at the distal part of the thallus, the upper (distal) one is the smaller at 2·67 mm (Fig. 5), the lower (proximal) one being larger at 4·16 mm (Fig. 6). This indicates that the thallus diminishes in diameter near the top and may have been rounded at the end: Fig. 2. The calcareous wall of the thallus is rather thin, 0·20–0·35 mm, compared with that of the large central stem which is 3·20–3·68 mm in diameter. The internal diameter is thus up to 90% of the external diameter (Table 1).

The most remarkable feature of the thallus is the development of distinct outer and inner annulations (rings). Regularly spaced at 0·47–0·82 mm apart, these are 0·44–0·67 mm thick from inside to outside and 0·067 –0·16 mm wide vertically, with rounded or tapering edges; they project 0·067–0·20 mm on the inner and outer surface of the calcareous wall. These annulations resulted from extra development of branch-intervals (interpores). They grow horizontally, or slightly inclined upwards. Rounded depressions left by branches exist on the surface of the annulations, which can be seen in the longitudinal-tangential sections, Figs 3–4.

Branches (pores) are numerous and close-set, subcylindrical in shape, medially swollen,

Table 1 Dimensions of *Nanjinoporella*, Measurements in mm: D — outer diameter, d — inner diameter, p — pore diameter, ip — distance between pores, ia — distance between annulations, tha — thickness of annulation.

Sections	D	d	d/D	p	ip	ia	tha
Longitudinal (Fig. 3)	3·63–4·11	3·20–3·68	0·88–0·90	0·094–0·15	0·034–0·094	0·47–0·78	0·067–0·16
Tangential (Fig. 4)	–	–	–	0·11–0·16	0·027–0·11	0·64–0·82	0·067–0·11
Cross (Fig. 5), near distal end	2·67	2·07	0·78	0·054–0·08	0·067–0·12	–	–
Cross (Fig. 6), below Fig. 5	4·21	3·47	0·82	0·067–0·11	0·054–0·11	–	–



Figs 3–4 *Nanjinoporella pagoda* sp. nov. Lower Permian, Artinskian, Swine Limestone member, Chihsia Formation, Dawa, Chihsia Shan Hill, Nanjing, China. **Holotype**, PB.68055. Thin sections, ×12·4. Fig. 3, longitudinal section. Fig. 4, tangential section.

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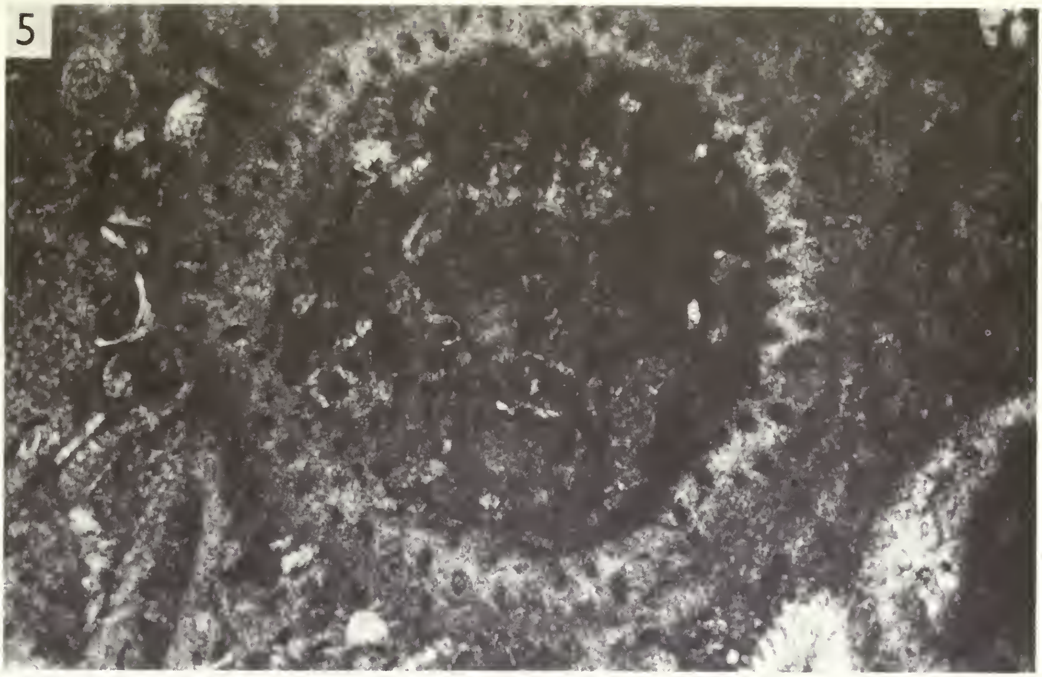

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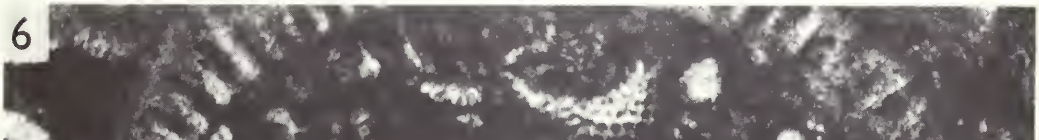

Figs 5–6 *Nanjinoporella pagoda* sp. nov. Lower Permian, Artinskian. Swine Limestone member, Chihsia Formation, Dawa, Chihsia Shan Hill, Nanjing, China. **Holotype**, PB.68055. Thin sections, × 31. Fig. 5, cross section near the distal end of the thallus. Fig. 6, another cross section below that shown in Fig. 5.

and with circular to elliptical cross sections, the longer axes of which are parallel with that of the thallus. They are 0·067–0·16 mm in diameter and slightly constricted at both ends. They grow at right angles to the axis of the thallus or are slightly inclined upwards, and open at both inner and outer surface of the calcareous wall.

Some differences exist in shape, size and arrangement between branches. Sometimes the branches next to the annulation, above and below, have their own calcareous sheaths with rounded closed terminal ends. Their lengths are the same as those of the annulations, longer than the rest of the branches. They are arranged in whorls, while the rest of the branches are irregularly set, or are locally spiral. The spaces between branches (interpores) are 0·27 to 0·12 mm. In longitudinal and tangential sections it can be seen that there are 4–5 rows of branches between consecutive annulations. Fig. 6 is a cross section just through the surface of an annulation, showing a whorl of branches. From a quarter of this section, 21 branches were counted, giving about 80 branches to a whorl.

Fig. 5 is a cross section near the top of the thallus. There are two rows of rounded pores alternately arranged within the calcareous wall, showing that the branches near the top of the thallus become thinner and incline upwards, a common dasyclad feature.

HOLOTYPE. The specimen (Figs 3–6) is from the Swine Limestone member of the Chihsia Formation, Artinskian, Lower Permian; Dawa, Chihsia Shan Hill, Nanjing, China. It is housed in the palaeobotany collection of Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China. Field collection no. D 501-H 12-5; registration no. PB.68055.

DISCUSSION. The present plant has a long near-cylindrical club-shaped thallus with rounded distal termination. It is not known, however, whether the top of the skeleton of the plant was open or closed. The suggestion that it was closed is proposed here, by analogy with *Epimastopora malaysiana* Elliott (1968*a*) which is most similar to the present form (see below).

Epimastopora malaysiana is represented by a nearly complete solid specimen with the distal end of the skeleton worn away. Judged from the fact that the surface of the top of the core (filling) is quite smooth, it is believed that the top of the skeleton was closed. If the top was open, the core would have been in direct contact with the external matrix, the removal of which from the fossil would have left a ragged rather than a smooth surface at the top of the core.

It is not clear whether the differences in the lengths of the branches are an original feature or result from different degrees of calcification.

Nanjinoporella is characterized by its unique annulation structure, not known in other dasyclads. However, to some extent it can be compared with certain members of *Epimastopora* Pia, 1922 (cf. *Paraepimastopora* Roux, 1979), among which *E. malaysiana* is the most similar. In being a very large dasyclad with thin calcareous wall, *E. malaysiana* resembles *Nanjinoporella pagoda* in many respects, such as the general shape of the thallus and pores, the ratio of internal to external diameter, the dimensions of pores and interpores, etc. The most remarkable feature of *E. malaysiana* is the existence of internal annulation which results from the intervals between zones of pores, similar to those of *Nanjinoporella pagoda*, but represented by regularly-spaced horizontal sinuous grooves on the surface of the inner core. These inner annulations separate the pores into fascicules of six or seven rows. There is also a trend towards arrangement of the branches into whorls. Paired rows of branches just above and beneath the annulations form horizontal whorls, while the rest of the branches are aspondyl. This pattern is somewhat similar to *Nanjinoporella pagoda.*

Among other differences between these two forms is the basic one that in *Epimastopora malaysiana* there are no outer annulations separating paired rows of euspondyl branches as in *Nanjinoporella pagoda*, except for horizontal lines which correspond in position to the inner annulations. But it is evident that phylogenetically these two forms are very closely related to each other.

A phylogenetic lineage suggested here is that *Nanjinoporella* might have originated from typical *Epimastopora* through an intermediate link such as *Epimastopora malaysiana.* This evolutionary advance would be achieved by two or three steps. Firstly, an *Epimastopora* with aspondyl branches would give rise to a form with regularly spaced, paired rows of euspondyl branches with smooth intervals left between them. At the same time or a little later these intervals would extend inside to form inner annulations resulting in a new form like *Epimastopora malaysiana.* Finally, these annulations would extend outside to give rise to the outer annulations seen in *Nanjinoporella.*

Since no descendants of *Nanjinoporella* have been found so far, it is assumed that it might represent a specialized side branch in the phylogenetic tree of *Epimastopora*, and *E. malaysiana* may be regarded as an intermediate link connecting typical *Epimastopora* with *Nanjinoporella.*

At present it is difficult to say if *Nanjinoporella* originated directly from *Epimastopora malaysiana* because they are both found in rocks of the same age and more information is needed about their geological ranges. However, it is reasonable to suggest that at least they came from a common ancestor which might be expected in pre-Permian times.

The difficulty in discussing dasyclad phylogeny is that what we are dealing with today are only the calcified skeletons of plants and these vary greatly in the degree of calcification. Hence it is often not known how much is lost. It is not safe to reconstruct evolutionary paths exclusively from the information available from these skeletons. It is quite possible that most of the soft parts of the plant did not leave skeleton traces (cf. Kozlowski & Kaźmierczak 1968, for *Vermiporella*). It is evident that the foregoing suggestion of the phylogeny of *Nanjinoporella* is very tentative and open to emendation according to possible new data available in the future.

Annulation structures in dasyclads

Annulation structures are common in dasyclads, but they vary both in position and in origin between different taxa. The type of annulation developed in most dasycladales may be related to periodic algal growth followed by calcification, which in some other algae results in segmentation. The original random development of branches over the stem-cell surface (aspondyl condition) is modified by:

1. Grouping of branches into annular zones, as in *Epimastopora malaysiana.*
2. Emphasis of this by solid partitions (inner and outer), as in *Nanjinoporella.*
3. Normal verticillate structure, which may be reinforced by (a) external annular calcifications of different types round verticils of branches, as in *Clypeina*, *Pseudocymopolia* etc., or (b) inner annular calcification connected with periodic swelling (waxing and waning) of the stem-cell, as in *Diplopora phanerospora* etc.

It is worth pointing out that *Nanjinoporella* is the only known dasyclad with both inner and outer annulations resulting from the extension of calcareous intervals between branches, and this unique feature makes it clear-cut and distinguishable from other dasyclads.

Annulation structure is given different importance in the classification of dasyclads by different authors. Some authors claim that this kind of structure does not even have specific value (Bassoulet *et al.* 1977). However, others use it as an important criterion to distinguish between different tribes, e.g. the Beresellae and Palaeoberesellae (Mamet & Roux 1974), although it is not certain if the latter are true dasyclads. In the present case it is used as a diagnostic criterion at generic level.

The function of the annulation of *Nanjinoporella* is not known; this is related to our ignorance of the significance of calcification to the algae. Calcification may strengthen plants mechanically or shield them from high solar radiation, predators etc., but the fact remains that we don't know why they calcify because uncalcified algae flourish side by side with calcified ones in the same environment. Moreover, all the complexities of dasyclad calcification have not prevented their decline to a very subordinate position in the present-day marine flora, compared with that which they held in the past. *Halimeda* has gained at their expense (Elliott 1968*b*).

Acknowledgements

This paper was prepared in the Department of Palaeontology of the British Museum (Natural History), London, during Mu Xinan's visit to Britain which was arranged by the Royal Society and the Chinese Academy of Sciences.

We would like to thank Mr Min Qing-kui, Regional Geological Survey Team of Anhui, China, for providing the material on which this study is based; Mr Ji Cheng-dao, of the Rock-cutting Laboratory of Nanjing Institute of Geology and Palaeontology, Academic Sinica, for the preparation of thin sections; Mr C. H. Shute for photographs of specimens; and Mr M. Crawley for redrawing Figs 1 and 2 for reproduction.

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Toarcian bryozoans from Belchite in north-east Spain

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Synopsis

A small fauna of bryozoans is described from the Upper Toarcian of Belchite near Zaragoza, Spain. *Microeciella* gen. nov. is proposed for bereniciform tubuloporinids previously assigned to *Microecia* but differing from the type species of that genus in having small gonozooids with ovate dilated portions. Together with the type species of *Microeciella*, *M. beliensis* sp. nov., the Belchite bryozoans consist of *M. reflexa* sp. nov., '*Proboscina*' cf. *divisi* Vine and an undetermined bereniciform tubuloporinid. *M. reflexa* is unusual in having an erect ancestrular tube from which a daughter zooid descends to re-establish contact with the substrate. The identity of various genera used for tubuloporinids of the '*Berenicea*' type is discussed.

Introduction

Few records exist of Jurassic bryozoans from countries other than England, France and Germany, and the great majority of described species occur in rocks of mid-Jurassic age. These geographical and stratigraphical limitations inhibit a close understanding of bryozoan evolution at a time when the Cyclostomata were entering an important period of diversification. Therefore, the discovery of a small but well-preserved bryozoan fauna from the Toarcian of Spain is significant and warrants description in this short paper. It also provides the opportunity to discuss the identity of several genera which have been proposed to subdivide so-called '*Berenicea*', a bryozoan ubiquitous in the Jurassic.

Material is deposited in the palaeontological collections of the British Museum (Natural History), abbreviated BM(NH), and in the collections of the Departamento de Paleontologí́a, Universidad de Zaragoza, abbreviated UZ. All figured material is in the BM(NH).

Previous records of Toarcian bryozoans

When describing a small bryozoan fauna from the Toarcian of Banne in the Saône-Rhône Basin of France, Walter (1970 : 244) remarked on the rarity of bryozoans in Toarcian deposits. The Banne bryozoans are of early Toarcian age (*falciferum* Zone) and consist of *Radicipora radiciformis* (Goldfuss) and *Neuropora* sp., the latter now considered to be a sclerosponge genus (Kaźmierczak & Hillmer 1974). Also from France, Dumortier (1874) described two species from Crussol: *Diastopora crussolensis* is a discoidal bereniciform tubulorporinid but his figures (Dumortier 1874 : pl. 48, figs 11, 12) do not reveal the presence of gonozooids necessary for a more up-to-date generic attribution; *Berenicea garnieri* is indeterminable from the figure (1874 : pl. 48, fig. 13) and may not even be a bryozoan.

From the 'Ob. Lias' Quenstedt (1852 : 637; pl. 56, fig. 10) described *Diastopora liasica*, a straggly prosbosciniform tubuloporinid without visible gonozooids.

Spiropora liassica Tate, 1875, is an erect, vinculariiform cyclostome which occurs in the

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U. Pliensbachian of England but was also recorded by Tate in the Toarcian '*Leptaena*' Bed at May in Normandy.

Walford (1887) described *Tubulipora inconstans* from the Transition Bed (Toarcian) at Appletree near Banbury, and Badby near Daventry, both in the English Midlands. This erect cyclostome was placed in synonymy with *Mesenteripora wrighti* Haime, 1854, by Walter & Powell (1973).

One of the few Jurassic bryozoans hitherto recorded from North America is *Heteropora tipperi* Henderson & Perry from early Toarcian rocks in British Columbia (Henderson & Perry 1981).

Including the species described in the present paper, the worldwide diversity of Toarcian bryozoans so far described amounts to about 10 species. However, these include a fairly wide variety of forms, suggesting that a much greater number of species lived in Toarcian times than is evident from current knowledge of the fossil record.

The Toarcian of Belchite

Belchite is situated 40 km SSE of Zaragoza in the north-east of Spain. A Jurassic sequence of Sinemurian to Bathonian age has been described by Sequeiros *et al.* (1978). Bryozoan-encrusted shells of the large bivalve *Plagiostoma* occur in the 3 m of rock designated Beds 29–34. These lie within the upper part of the Turmiel Marls Formation (Goy *et al.* 1976) and are Upper Toarcian. The ammonites from Beds 29–34 suggest that they span the *variabilis*, *thouarsense*, *insigne* and *pseudoradiosa* Zones.

Sequeiros & Mayoral (1982) and Mayoral & Sequeiros (1981) have studied the palaeoecology of the encrusting epifauna and boring infauna of shells from various parts of the Belchite succession. A sample of almost 100 *Plagiostoma* shells has been collected from the U. Toarcian. Although Mayoral & Sequeiros (1981) regarded these as *P. gigantea* (Sowerby) they differ from the type specimen of this species and are more appropriately named *P.* cf. *hersilia* (d'Orbigny). The shells are encrusted by serpulids (*Dorsoserpula, Cycloserpula, Tetraserpula*), thecidean brachiopods, cemented bivalves and the bryozoans described herein which Mayoral & Sequeiros (1981) identified provisionally as *Berenicea* sp. and *Stomatopora* sp. Scanning electron microscopy undertaken during the present study has revealed two additional encrusters, a planispirally-coiled foraminifer and a straight tubular microfossil that may also be a foraminifer.

Systematic descriptions

Order **CYCLOSTOMATA** Busk, 1852

Suborder **TUBULOPORINA** Milne-Edwards, 1838

? Family **ONCOUSOECIIDAE** Canu, 1918

Genus ***MICROECIELLA*** nov.

DIAGNOSIS. Tubuloporina with multiserial colonies, fan-shaped or discoidal (bereniciform); gonozooids small with a long proximal frontal wall similar to that of autozooids, and a dilated distal frontal wall which is longitudinally ovate in outline; ooeciopores small, circular or transversely elongate, located subterminally.

TYPE SPECIES. *Microeciella beliensis* sp. nov.; L. Jurassic (U. Toarcian) of Belchite, near Zaragoza, Spain.

REMARKS. Jurassic bereniciform and probosciniform tubuloporinids having small gonozooids with longitudinally ovate dilated frontal walls and small ooeciopores have been assigned (e.g. Walter 1970, Taylor 1981) to *Microecia* Canu, 1918. This assignment is now considered to be unsuitable because the type species of *Microecia* by original designation, the living *Diastopora sarniensis* Norman, 1864, has large gonozooids with broad dilated frontal walls penetrated by autozooids. However, in his original description of *Microecia*, Canu (1918) noted its small gonozooids. The other extant species referred by Canu to *Microecia* is *Diastopora suborbicularis* Hincks, 1880, which does have gonozooids matching those of Canu's description. For this reason Harmelin (1976*a*) proposed that *D. suborbicularis* should replace *D. sarniensis* as the type species of *Microecia*. Harmelin acknowledged that a decision of the I.C.Z.N. would be needed to validate this substitution. In its absence the genus *Microecia* is defined by its valid type species *D. sarniensis* which Harmelin (1976*a*: 136) considers to be a species of *Plagioecia* Canu, 1918. The gonozooid of *D. suborbicularis* suggests affinities with *Hyporosopora* Canu & Bassler, 1929 (see p. 127).

Microeciella is here proposed for bereniciform tubuloporinids with small gonozooids having longitudinally ovate dilated frontal walls. Apart from the type species, *M. beliensis* sp. nov., two other Jurassic species are referred to *Microeciella*, *M. reflexa* sp. nov. and *Microecia matisconensis* Walter, 1970. Probosciniform tubuloporinids with similar gonozooids (e.g. *Diastopora belemnitarum* d'Orbigny, 1850, *Microecia southwellensis* Taylor, 1981, *Proboscina ornata* Vine, 1893, all from the Jurassic) may require a second new genus but their revision is beyond the scope of this paper.

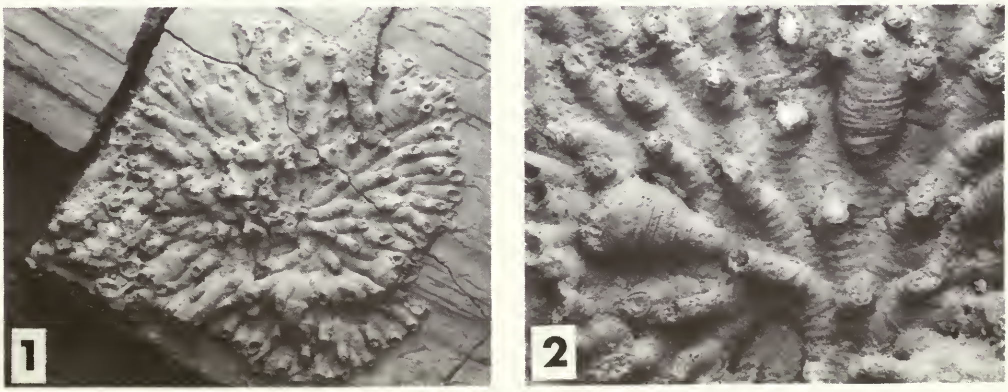
Gonozooids of *Microeciella* differ minimally from autozooids; the distal, densely pseudoporous frontal wall of the gonozooid is dilated to a comparatively small degree and is preceded by a long, proximal frontal wall which is indistinguishable from the frontal wall of an autozooid. Gonozooids occupy the same budding position as autozooids. Therefore, on the assumption that bryozoan gonozooids evolved from autozooids by progressive partitioning of reproductive function within colonies and concomitant morphological differentiation, the gonozooids of *Microeciella* may be regarded as primitive for the Tubuloporina. This inference is supported by the stratigraphically early occurrence of the genus. The gonozooids of *Microeciella* would appear to be more primitive than the tiny gonozooids budded on the peristomes of some living stomatoporids (Harmelin 1974) which were considered by Harmelin (1976*b*: 612) to represent the most primitive form of tubuloporinid gonozooid.

Microeciella beliensis sp. nov.

Figs 1, 2, 8, 10

DIAGNOSIS. *Microeciella* having small autozooids and gonozooids with circular ooeciopores.

HOLOTYPE. BM(NH) D.53321, colony a (Figs 1, 13); U. Toarcian, Belchite, Zaragoza, Spain. L. Sequeiros Coll.



Figs 1, 2 *Microeciella beliensis* gen. et sp. nov. U. Toarcian, Belchite, Spain. Fig. 1, **holotype**, D.53321, colony a; ×10. Fig. 2, paratype, D.53321, colony b, showing two gonozooids; ×27. Together with Figs 3–5, these are scanning electron micrographs of uncoated specimens taken using back-scattered electrons in a CFACS environmental chamber.

PARATYPES. BM(NH) D.53321, colonies b (Fig. 2), c; UZ SBE-4(a–c), SBE-10, SBE-17(a, b). All U. Toarcian, Belchite.

DESCRIPTION. Colony small (generally <5 mm in diameter), encrusting, multiserial, bereniciform – initially fan-shaped but becoming discoidal (Fig. 1) with 'windows' of substrate visible between early zooids and lateral lobes of the fan. Ancestrula overgrown by later zooids. Fan-shaped peripheral subcolonies may develop between areas of inactive growth margin.

Autozooids slender, frontal walls about 0·80 mm long and 0·20 mm wide. Apertures are longitudinally elongate, small, their diameter varying between 0·14 × 0·12 mm and 0·08 × 0·06 mm depending on preservation of the peristome which tapers distally and has a maximum observed length of 0·23 mm. Peristome inclined at an acute angle to the colony surface. Terminal diaphragms and ontogenetic zonation not apparent.

Table 1 Gonozooid dimensions (mm) in *Microeciella beliensis* gen. et sp. nov. Abbreviations: $\bar{x}$ = mean; SD = standard deviation; CV = coefficient of variation; Nz = number of gonozooids measured; Nc = number of colonies sampled; R = observed range; tgl = total length of gonozooid frontal wall; igl = length of inflated distal frontal wall; gw = width of frontal wall (maximum).

	$\bar{x}$	SD	CV	Nz	Nc	R
tgl	1·10	0·137	12·5	14	5	0·75–1·28
igl	0·65	0·083	12·8	16	6	0·51–0·78
gw	0·37	0·022	6·0	15	6	0·33–0·41

Gonozooids (see Table 1 for dimensions) present in all colonies examined. A long proximal frontal wall, indistinguishable from that of an autozooid, gives rise to a dilated, distal frontal wall, which is small and ovate to subpyriform (Fig. 2), and densely pseudoporous. Ooeciopore located subterminally, smaller than autozooid apertures, approximately circular and 0·05–0·06 mm in diameter. Ooeciostome curved slightly proximally, maximum observed length 0·08 mm.

REMARKS. The trivial name *beliensis* derives from the Roman city of Belia, which was situated close to the type locality of Belchite.

Microeciella matisconensis (Walter) resembles *M. beliensis* but the gonozooid of this French Callovian species differs from that of *M. beliensis* in being wider (0·50–0·60 mm) and in having a marked constriction between the proximal and distal dilated portions of the frontal wall.

Microeciella reflexa sp. nov.

Figs 3–5, 7–8

DIAGNOSIS. *Microeciella* having autozooids of moderate size; gonozooids constricted and arched at the transition between proximal and distal inflated frontal wall; ooeciopores transversely elliptical; erect ancestrular tube budding a second generation zooid which descends to the substrate and grows at 90° to the principal growth direction of the ancestrula.

HOLOTYPE. BM(NH) D.53320, colony a (Figs 3, 4, 11); U. Toarcian, Belchite, Zaragoza, Spain. L. Sequeiros Coll.

PARATYPES. BM(NH) D.53320, colonies b–m (Figs 6, 7, 11); D.53321, colony d (Figs 5, 13), D.53323, S.E.M. stub (Figs 9, 10) and colonies a–b; D.53324a–b, D.53325, D.53326 (Fig. 12), UZ SBE-4(d), SBE-6, SBE-23, SBE-24. All U. Toarcian of Belchite.

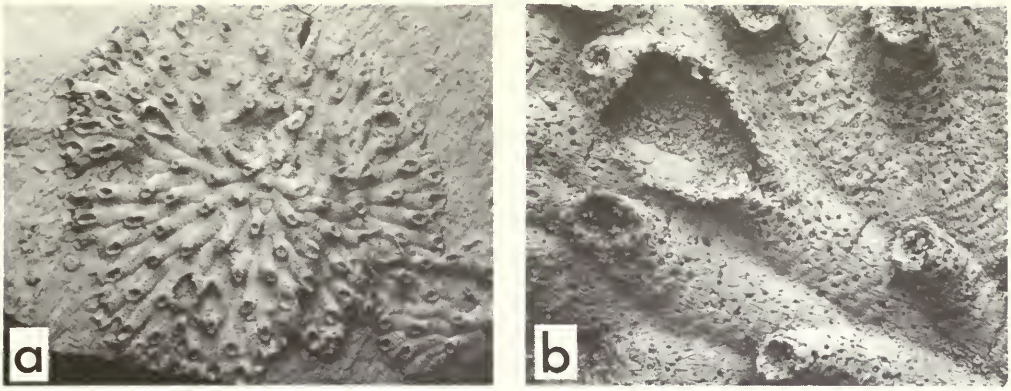


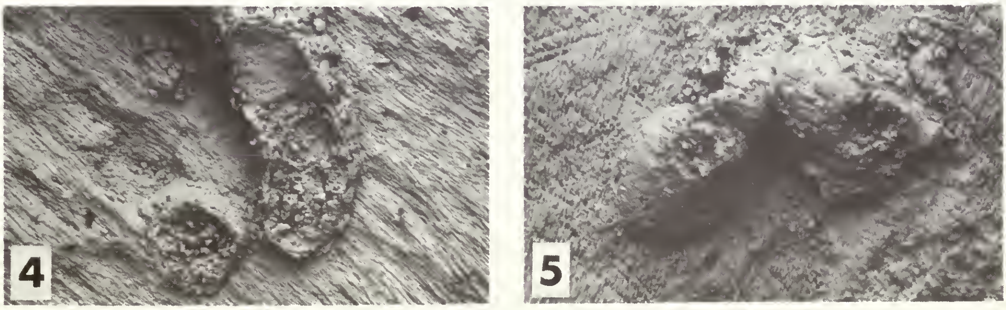
Fig. 3 *Microeciella reflexa* gen. et sp. nov. U. Toarcian, Belchite, Spain. **Holotype**, D.53320, colony a. a, general view of colony; ×6. b, gonozooid with dilated part of frontal wall abraded; ×40.

Description. Colony encrusting, multiserial, fan-shaped or discoidal bereniciform (Fig. 3a). Peripheral fan-shaped subcolonies may develop, some overgrowing earlier zooids. There is a substantial increase in zooid size during early astogeny.

Protoecium 0·17–0·20 mm in diameter, giving rise to an obliquely inclined erect ancestrular tube which is free of the substrate (Fig. 6). The ancestrula, overgrown in large colonies, buds a second generation zooid which descends to re-establish contact with the substrate. In abraded colonies (Fig. 5a) the resultant break in continuity of the basal lamina between protoecium and the remainder of the adnate colony is clearly seen. Zooid budded from the ancestrula is orientated at about 90° to the growth direction of the ancestrula (Fig. 5b). This bend in growth direction is left-handed in some colonies, right-handed in others.

Autozooids moderately large, elongate, with frontal walls averaging in length 0·92 mm (observed range 0·71–1·16 mm) and in width 0·23 mm (observed range 0·20–0·27 mm). Apertures longitudinally elongate, up to 0·20 × 0·12 mm in autozooids lacking peristomes but smaller when the distally tapering peristome is preserved. Peristomes bend to become almost perpendicular to the colony surface. Some autozooids possess terminal diaphragms though ontogenetic zonation is not clearly developed.

Gonozooids developed in a minority of colonies (see Table 2 for dimensions). A long proximal frontal wall, indistinguishable from that of an autozooid, gives rise to a dilated distal frontal wall, small and ovate to subpyriform in outline shape. Frontal wall is arched



Figs 4, 5 *Microeciella reflexa* gen. et sp. nov. U. Toarcian, Belchite, Spain. Early growth stages (cf. Fig. 6). Fig. 4, paratype, D.53320, colony a, abraded specimen showing break in continuity between protoecium and second zooid on the substrate; ×70. Fig. 5, paratype, D.53320, colony m, small colony consisting of protoecium, erect ancestrular tube, and a second zooid which is orientated at 90° to the ancestrula; ×67.

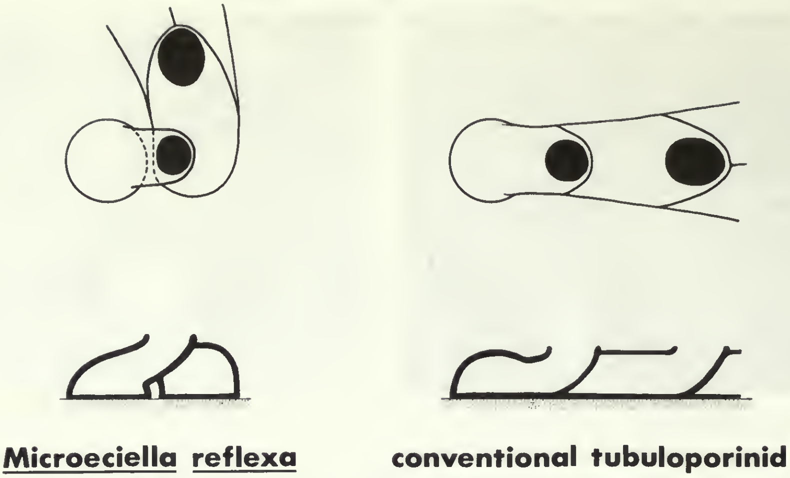


Fig. 6 Diagram contrasting the early growth stages of *Microeciella reflexa* gen. et sp. nov. and a conventional tubuloporinidean cyclostome. Colonies are shown in surface view (above) and in vertical section (below). In *M. reflexa* an erect ancestrular tube, free of the substrate (stippled), arises from the protoecium. Budded from the ancestrula is a second generation zooid which descends to the substrate and is orientated at 90° to the ancestrula.

Table 2 Gonozooid dimensions (mm) in *Microeciella reflexa* gen. et sp. nov. For abbreviations see Table 1.

	$\bar{x}$	SD	CV	Nz	Nc	R
tgl	1·22	0·092	7·6	8	3	1·05–1·35
igl	0·56	0·120	21·3	9	3	0·39–0·80
gw	0·38	0·044	11·7	10	3	0·32–0·45

upwards (Fig. 7b) and somewhat constricted in width (Fig. 7a) between proximal and distal parts of the gonozooid. Ooeciopore subterminal, transversely elliptical (Fig. 3b), and at about 0·07 × 0·09 mm in diameter, smaller than autozooid apertures. Ooeciostomes not preserved.

REMARKS. This species is characterized by its distinctive early growth stages with an erect ancestrular tube and a second generation zooid bent or 'reflexed' by about 90° to the growth direction of the ancestrula.

M. reflexa is distinguished from *M. beliensis* by the larger size of its autozooids, apparent in Fig. 13, and the arched and constricted transition between proximal and distal parts of the gonozooid frontal wall which is very similar in size in both species (compare Tables 1 and 2). Colonies of *M. reflexa* are often larger than those of *M. beliensis* but some gonozooids are less frequently developed. Like *M. beliensis*, *M. reflexa* differs from *M. matisconensis* (Walter) in having narrower gonozooids. Details of early astogeny, another potential distinguishing feature, are unknown in both *M. beliensis* and *M. matisconensis*.

Family **STOMATOPORIDAE** Pergens & Meunier, 1886
'Genus ***PROBOSCINA*** Audouin, 1826'
'***Proboscina***' cf. ***divisi*** Vine, 1893

MATERIAL. BM(NH) D.53327, colony a; UZ SBE-6, SBE-8, SBE-13. U. Toarcian, Belchite, Zaragoza, Spain. L. Sequieros Coll.

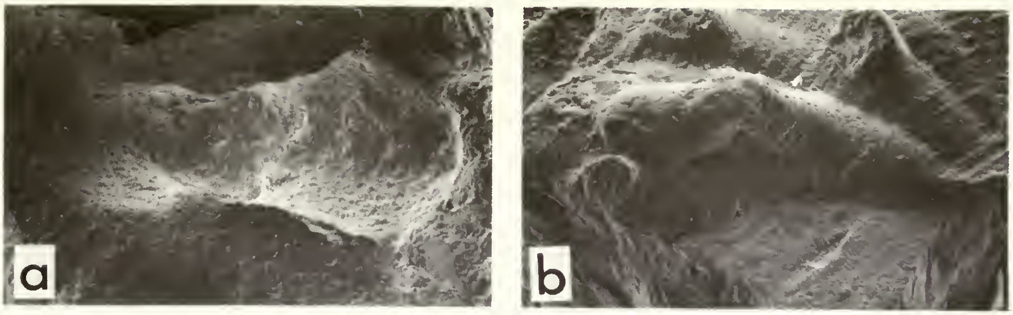
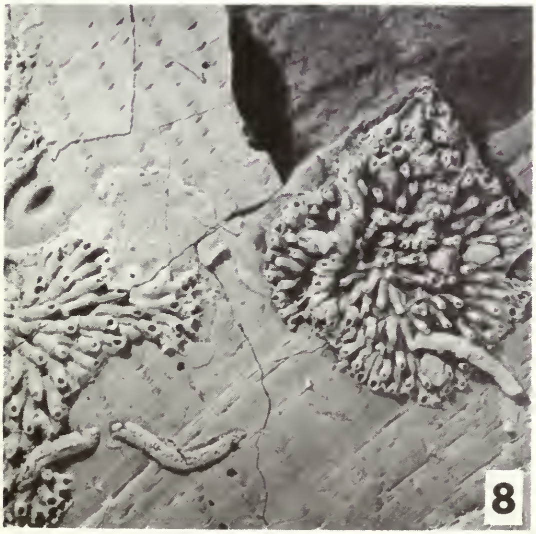
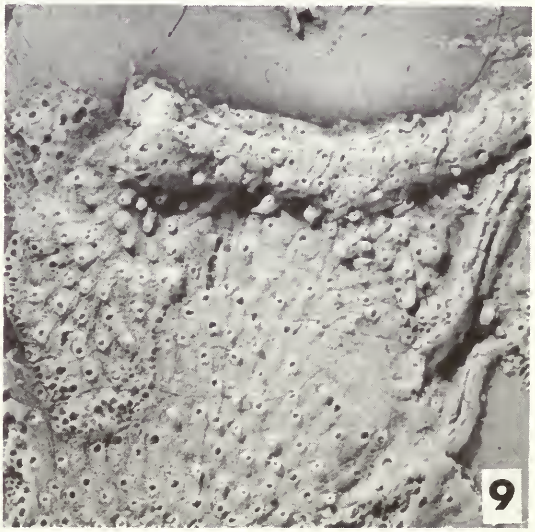


Fig. 7 *Microeciella reflexa* gen. et sp. nov. U. Toarcian, Belchite, Spain. Gonozooid morphology. Scanning electron micrographs of coated paratype, D.53323. a, gonozooid viewed from above showing constriction between proximal and distal dilated parts of the frontal wall; ooeciopore obscured by sediment; ×70. b, the same gonozooid viewed in oblique profile illustrating the arched transition between proximal and distal dilated parts of the frontal wall; ×40.

Description. Colony encrusting, consisting of narrow, multiserial, bifurcating branches (probosciniform), about 0·3–0·7 mm and 3–4 zooids wide. Early (? first) angle of bifurcation is 180°, later bifurcations are generally less than 90° and sometimes asymmetrical. Branches apparently flanked by kenozooids which taper in height towards the edge of the branch.

Autozooids with slightly convex frontal walls averaging about 0·71 mm in length (observed range 0·62–0·82 mm) and 0·20 mm in width (observed range 0·18–0·23 mm). Apertures longitudinally elongate, about 0·14 × 0·11 mm in zooids lacking peristomes. Peristomes up to 0·15 mm long, distally tapering, and curved until approximately perpendicular to the colony surface. Gonozooids absent.





Figs 8, 9 Photomicrographs of bryozoans from the U. Toarcian of Belchite, Spain. Fig. 8 (left), D.53321, colony d, paratype of *Microeciella reflexa* gen. et sp. nov., and (right) D.53321, colony a, holotype of *Microeciella beliensis* gen. et sp. nov. Illustrating the difference in zooid size between the two species; ×8. Fig. 9, D.53327, colony b, the undetermined bereniciform tubuloporinid; after overgrowing a serpulid, a lobe of the colony has spiralled back to overgrow earlier-formed zooids (centre left); slightly beneath centre right is an area of the colony composed of kenozooids and devoid of apertures; ×6.

REMARKS. This species is represented by four poorly-preserved colonies. They resemble *Proboscina divisi* Vine, 1893, described from the Bathonian of Thrapston in Northamptonshire, but zooid size in the Belchite bryozoans is slightly smaller than in Vine's type specimen of *P. divisi* (BM(NH) D.31142).

Jurassic palaeontologists (e.g. Vine 1893, Gregory 1896*b*) have traditionally used the name *Proboscina* for tubuloporinids with adnate colonies in which the zooids are arranged in narrow, multiserial, bifurcating branches – i.e. the probosciniform growth-form (see Taylor, 1976 : text-fig. 2B). *Proboscina* was founded by Audouin (1826) for living cyclostomes having this colony growth-form. The type species, *P. boryi* Audouin, has well-developed gonozooids. However, in many Jurassic species, including the one from Belchite, gonozooids are unknown. These species seem either to have lacked gonozooids or perhaps to have had gonozooids which were budded high on the delicate peristomes of autozooids (Harmelin 1974) and not fossilized. Their assignment to *Proboscina* is inappropriate but the creation of a new generic name must await description of a more complete and better preserved suite of specimens than that from Belchite. In the meantime, '*Proboscina*' is written in quotations.

Family uncertain

Undetermined bereniciform tubuloporinid

Fig. 9

MATERIAL. BM(NH) D.53327, colony b; U. Toarcian, Belchite, Zaragoza, Spain. L. Sequeiros Coll.

DESCRIPTION. A single large colony, encrusting, multiserial (bereniciform), with a lobate expansion which spirals proximally to overgrow earlier-forward zooids. Early astogenetic zones not preserved.

Autozooids large with frontal walls averaging 1·11 mm in length (observed range 0·90–1·43 mm) and 0·31 mm in width (observed range 0·27–0·33 mm). Apertures longitudinally elongate in zooids lacking peristomes, smaller and approximately circular in zooids preserving distally tapering peristomes.

Kenozooids numerous, some occurring singly between autozooids, others aggregated. They are smaller and narrower than autozooids, and lack apertures. Gonozooids lacking.

REMARKS. The absence of gonozooids in this single specimen precludes generic identification. The colony and its constituent zooids are significantly larger than those of the other Belchite species. This colony could represent a later growth stage of *M. reflexa* if the zone of astogenetic increase in zooid size is very extensive in *M. reflexa*. However, the occurrence of numerous kenozooids, unknown in *M. reflexa*, may suggest that the specimen is a separate species.

Generic attribution of '*Berenicea*' species

With the proposal of the new genus *Microeciella* it is opportune to evaluate the generic attribution of the numerous tubuloporinid species which are conventionally referred to *Berenicea*. The genus *Berenicea* has been used for sheet-like encrusting tubuloporinids of Ordovician to Recent age, though Palaeozoic examples are now regarded as *Sagenella* Hall (see Brood, 1975). However, the precise identity of *Berenicea* is a matter of contention, and it is clear that the name has been applied to a wide diversity of species varying in their affinities to one another and to other tubuloporinids.

Berenicea was proposed by Lamouroux (1821 : 80) when describing three new species, *B. prominens* and *B. annulata* from the Recent, and *B. diluviana* from the Jurassic. Lamouroux did not designate a type species. *B. prominens* is usually quoted as the type species of *Berenicea* (e.g. Bassler 1953, Brood 1972). However, the earliest designation of *B.*

prominens as type species appears to have been by Gregory (1896*a*), postdating a designation of *B. diluviana* made by Reuss (1867). Therefore, *B. diluviana* has priority and is the valid type species of *Berenicea*. As with *B. prominens* (see Brood, 1972 : 176), the identity of *B. diluviana* is obscure; Lamouroux's figures of the species are extremely stylized and his original material is said by Walter (1970) to have been lost during a fire at Caen in 1944. *B. diluviana* could be any of a number of species, now assigned to several genera, which occur in the type region of Caen. Therefore, the genus *Berenicea* is best regarded as a *nomen dubium*.

Diastopora, also proposed by Lamouroux (1821), has been used as an alternative to *Berenicea* by many bryozoologists. The type species by monotypy of this genus is *Diastopora foliacea* Lamouroux from the Jurassic. Walter's (1970) redescription, based on a neotype and other specimens, shows *D. foliacea* to have large erect colonies of unilamellar branches forming wide tubes or foliaceous fronds. Therefore, *Diastopora* is unsuitable as a substitute for so-called *Berenicea* whose colonies are encrusting and typically small.

Species of '*Berenicea*' are most easily discriminated using characters of the gonozooid. These show much greater variability between putative species than do the relatively uniform and simple autozooids. Gonozooidal characters were used by Canu (1918) and Canu & Bassler (1922, 1926, 1929) as the basis for several new genera and families. The systematic work of Canu & Bassler has been severely critized (e.g. Harmer 1931) and the validity of their cyclostome genera questioned (e.g. Brood 1972). Many of Canu & Bassler's taxa seem to have been founded on trivial differences but this should not lessen the value of gonozooidal characters for recognizing groupings of species regarded as genera. The identity and validity of these 'gonozooid genera', and of a few earlier genera of '*Berenicea*' type, rests on their defining type species. The following genera may be considered.

1. *Rosacilla* Roemer, 1840. The type species of this genus, given by Bassler (1935 : 192), is *Aulopora flabelliformis* Roemer, 1839 from the German Cretaceous. (This is not to be confused with *Cellepora flabelliformis* von Hagenow, 1839, the species listed first by Roemer (1840) in his description of *Rosacilla*, which may be the same as *Diplosolen pavonius* Voigt, 1929 (Voigt 1959).) Hillmer (1971 : 72) redescribed *A. flabelliformis* Roemer, noting the absence of gonozooids in the type material he studied. Gonozooids tend to be developed in only a small minority of colonies belonging to any particular cyclostome species known to have gonozooids and this may account for their absence in available specimens of *A. flabelliformis*. However, if it were to be established by examining a large, preferably topotype, population of *A. flabelliformis* that the species did not possess gonozooids, then *Rosacilla* may be an appropriate genus for species of '*Berenicea*' lacking gonozooids.

2. *Reptomultisparsa* d'Orbigny, 1853. This was created for multilamellar tubuloporinids resembling *Berenicea*. Without naming a type species d'Orbigny (1853) referred five species to the genus: *Diastopora diluviana* Milne-Edwards, 1838 (*non Berenicea diluviana* Lamouroux)', an opinion shared by later revisers (Buge & Fischer 1970; Walter 1970). As three new species *Reptomultisparsa dutempleana*, *R. glomerata* and *R. congesta* from the Cretaceous. D'Orbigny (1853) placed his own earlier species *Diastopora incrustans* d'Orbigny, 1850 in synonymy with '*Diastopora diluviana* Milne-Edwards (*non* Lamouroux)', an opinion shared by later revisers (Buge & Fischer, 1970; Walter, 1970). As Milne-Edwards (1838) did not intend his *Diastopora diluviana* to be a new species but merely a new generic attribution of *Berenicea diluviana* Lamouroux (the type species of *Berenicea* Lamouroux), *Diastopora incrustans* d'Orbigny is considered to be the valid name for this species. It was left to Gregory (1896*b* : 151) to designate the type species of *Reptomultisparsa*, giving it as '*R. microstoma* (Mich.), syn. *R. diluviana*, Edw. & Mich. (non Lamx.)'; i.e. Gregory placed *Diastopora microstoma* Michelin in synonymy with the species correctly called *Diastopora incrustans* d'Orbigny. This synonymy has not been accepted by later revisers (see Walter, 1970) and furthermore it is evident from a subsequent publication (Gregory 1896*c*) that the species called *Reptomultisparsa microstoma* (Michelin) by Gregory is *Diastopora incrustans* d'Orbigny. Therefore, Gregory misidentified *Diastopora microstoma* Michelin when designating it as the type species of *Reptomultisparsa*. In

accordance with Article 70(a) of the International Code of Zoological Nomenclature (see Buge & Fischer 1970), a case has been submitted to the Commission requesting that *Diastopora incrustans* d'Orbigny be designated as the type species of *Reptomultisparsa.* This distinctive species occurs as large multilamellar colonies on gastropod shells which are thought to have been occupied by hermit crabs (Buge & Fischer 1970). The gonozooids (Fig. 10) are very large, longitudinally elongate (fusiform) and have large ooeciopores.

3. *Dacryopora* Terquem, 1855. In a list of fossils from the Calcaire Ferrugineux (Jurassic) of Moselle, Terquem (1855 : 26) included *Dacryopora archiaci* Haime. This is the first use of the genus *Dacryopora* and the type species, by monotypy, is *Berenicea archiaci* Haime, 1854, a species which Haime described from material in the Terquem Collection of the Moselle region. Walter (1970 : 214) was unable to recover the type specimen of *B. archiaci* Haime from the Terquem Collection in the Paris School of Mines. Haime's original figures (1854 : pl. 9, figs 11a, b) are of a discoidal bereniciform colony with moderately large, longitudinally elongate gonozooids, apparently having a narrow distal 'neck' leading from the dilated frontal wall to an ooeciopore which is about the same size as the autozooidal apertures. With the exception of this unusual neck, the gonozooid in *Dacryopora* is similar in shape to that of *Reptomultisparsa*, but smaller. *Dacryopora* may perhaps be regarded as a junior synonym of *Reptomultisparsa.*

4. *Microecia* Canu, 1918. As discussed above (p. 119), the type species of this genus is the Recent *Diastopora sarniensis* Norman, 1864. This is regarded as a species of *Plagioecia* Canu, 1918 by Harmelin (1976*a*).

5. *Plagioecia* Canu, 1918. The type species of *Plagioecia* by original designation is the Recent *Tubulipora patina* Lamarck, 1816. The gonozooid, fully described by Harmelin

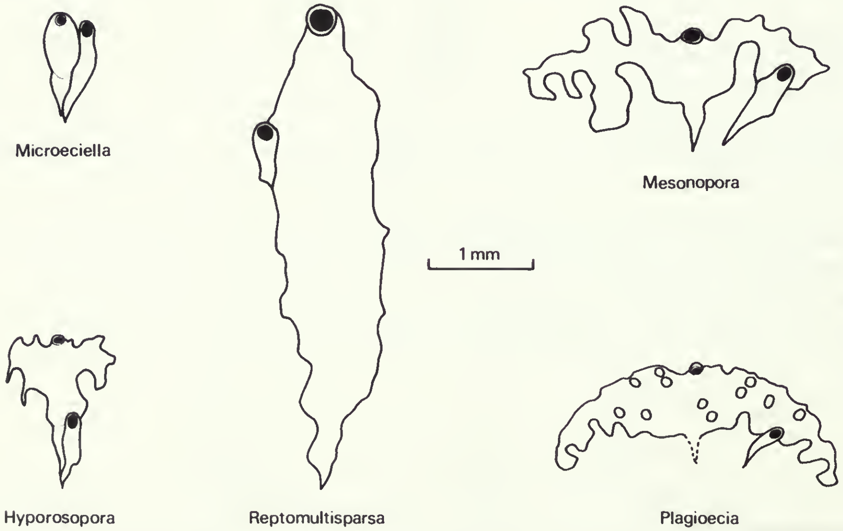


Fig. 10 Gonozooid morphology in various genera of bereniciform tubuloporinids drawn from specimens of type species. A single accompanying autozooid is shown in each case to give the relative scale of the gonozooid. The absolute scale is indicated by the 1 mm scale bar which applies to all gonozooids. Drawings were made from the following specimens: *Microeciella beliensis* gen. et sp. nov., paratype, D.53321, colony b; U. Toarcian, Belchite, Spain. *Hyporosopora typica* Canu & Bassler, D.13337; U. Bathonian (Bradford Clay), Bradford-on-Avon, England. *Reptomultisparsa incrustans* (d'Orbigny), D.53328; U. Bathonian, St Aubin-sur-mer, France. *Mesonopora concatenata* (Reuss) (= *Mesonopora typica* Canu & Bassler), 51342; U. Bathonian (Bradford Clay), Bradford-on-Avon, England. *Plagioecia patina* (Lamarck), Zoology Department 1976.8.14.14; Recent, Marseille, France.

(1976*a*), is broad and crescent-shaped (Fig. 10). Its margins are indented by autozooid apertures, some of which also pierce the frontal wall of the gonozooids away from the margins, and the terminal ooeciopore is transversely elongate with a proximally-directed ooeciostome.

6. *Diaperoecia* Canu, 1918. This genus has been used for Cretaceous–Recent tubuloporinids of varying colony-form, including species of '*Berenicea*' type and vinculariiform species of '*Entalophora*' type. By original designation the type species is *Pustulopora intricaria* Busk, 1875, a Recent tubuloporinid with a vinculariiform colony. It seems inappropriate to assign exclusively bereniciform species to this genus.

7. *Atractosoecia* Canu & Bassler, 1922. The original description of *Atractosoecia* includes two Jurassic species of which *Berenicea edwardsi* Canu, 1913, is cited as the type species. *B. edwardsi* is generally regarded as a junior synonym of *Diastopora incrustans* d'Orbigny (see Buge & Fischer 1970, Walter 1970). If *D. incrustans* is designated the type species of *Reptomultisparsa* by the I.C.Z.N. (see p. 126) then *Reptomultisparsa* and *Atractosoecia* share the same type species and *Atractosoecia* is a junior synonym.

8. *Mesonopora* Canu & Bassler, 1929. Two Jurassic species were included in the original description of this genus, *Mesonopora typica* Canu & Bassler, 1929, being given as the type species. Walter (1970 : 133) placed *M. typica* in synonymy with *Berenicea concatenata* Reuss, 1867. The gonozooid is broad, diffuse, and indented at its margins by apertures of autozooids (Fig. 10). The terminal ooeciopore is transversely elongate. Although similar to the gonozooid of *Plagioecia*, it lacks the distinct crescent-shape of the latter, and autozooids do not pierce the frontal wall away from the margins of the gonozooid.

9. *Hyporosopora* Canu & Bassler, 1929. By original designation the type species of *Hyporosopora* is *H. typica* Canu & Bassler, 1929, of Jurassic age. The gonozooid (Fig. 10) is moderately broad, subtriangular in outline, and has a small, transversely elongate ooeciopore located in a terminal position. In related Jurassic species subtriangular gonozooids were budded during early astogeny but later gonozooids developed forward-projecting lateral lobes giving the gonozooid a boomerang-shape (e.g. Taylor 1981 : text-fig. 3). *Hyporosopora* would appear to be a more appropriate name for certain Jurassic species previously assigned to *Plagioecia* (Walter 1970 : 117–128).

Of the 'gonozooid genera' discussed above the following are considered to be recognizable and potentially usable for species of the '*Berenicea*' type: *Reptomultisparsa* (large, longitudinally elongate gonozooids), *Plagioecia* (broad, crescentic gonozooids extensively pierced by autozooids), *Mesonopora* (broad, diffuse gonozooids), *Hyporosopora* (subtriangular or boomerang-shaped gonozooids), and *Microeciella* (small, ovate gonozooids). Further research is needed to establish the possible validity of *Rosacilla* for species lacking gonozooids. It should also be noted that many genera forming erect colonies may have early '*Berenicea*'-like growth stages. In addition some genera are diagnosed using characters unrelated to gonozooids, e.g. *Diplosolen* Canu for species with regular nanozooids and *Serpentipora* Brood for species with zigzag-shaped zooids.

Detailed morphological studies of cyclostome bryozoans (e.g. Boardman 1976) reveal the presence of new taxonomic characters which may eventually complement or supersede gonozooidal characters in classification. However, until the range and distribution of these characters is better understood, gonozooidal characters will remain the only convenient means of subdividing the plexus of species informally assigned to '*Berenicea*'.

Acknowledgements

We are grateful to Miss P. L. Cook for her critical comments, Dr B. Walter for providing information on *Microecia matisconensis*, Dr M. K. Howarth for stratigraphical advice, and Dr J. E. Whittaker and Mr C. P. Palmer for identification of associated foraminifers and bivalves respectively.

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Additional fossil plants from the Drybrook Sandstone, Forest of Dean, Gloucestershire

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Synopsis

New ovules are described showing sufficient internal structure to make them referable to *Carpolithus* Schlotheim, 1820, although as a new species *C. puddlebrookense.*

Lepidophyte stems previously called *Scutellocladus variabilis* are redescribed as being persistently leafy, ligulate and as having infrafoliar bladders. These characters make the stems referable to *Tomiodendron* Radczenko, emend. Meyen 1972. They are therefore rediagnosed as *T. variabilis* (Lele & Walton) comb. nov.

Introduction

The shale bed in the Drybrook Sandstone in Hazel Hill Quarry, near Puddlebrook, Forest of Dean is a well known locality of fossil plants. Allen (1961) described *Lepidostrobophyllum fimbriatum* Kidston from here while Lele & Walton (1962) described the rest of the then known flora of macrofossils and spores. More recently the moss *Muscites plumatus* Thomas (1971) has been found here. The miospore flora of the Drybrook Sandstone has also been investigated by Sullivan (1964) and shown to be comparable to that of the Oil Shale group of Scotland. The inference from this is that the Drybrook flora is of lower Upper Viséan age.

The present account deals with material that has been collected from the locality over many years. The very few specimens found indicate the relative scarcity of these plants in the shale bed. All the specimens are in the collections of the Palaeontology Department of the British Museum (Natural History).

Systematic descriptions

Division SPERMATOPHYTA

Form-genus *CARPOLITHUS* Schlotheim, 1820

Carpolithus puddlebrookense sp. nov.

Figs 1–3

Description. Four isolated ovules have been found from the Drybrook Sandstone of Puddlebrook Quarry. All are preserved as partially flattened casts with very little of their carbonized compression material having survived fossilization. They are virtually identical in size, being 4 mm in length and 2 mm in maximum width. Three have been split, on breaking the shale, showing the integuments to be 0·33 mm thick and fused to the nucellus except at the apex where they divide into four apical lobes. The possession of separate integumental lobes naturally precludes the possession of a micropyle, but one specimen (Figs 1, 2) shows signs of a salpinx with an underlying lagenostome and plinth. None shows any signs of integumental tissue differentiation into sarcotesta and sclerotesta but this is to be expected due to the limitations of preservation.

The four integumental lobes appear to be equal in size and therefore suggest that the ovules were originally radially symmetrical. Slight indications can be seen of longitudinal

Bull. Br. Mus. nat. Hist. (Geol.) **36** (2): 131–142

Issued 28 October 1982

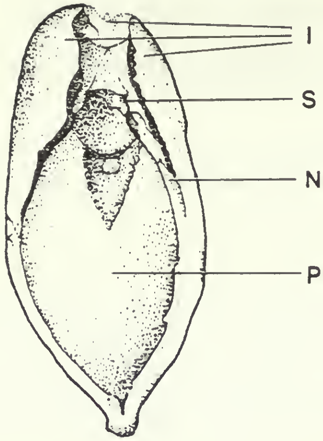
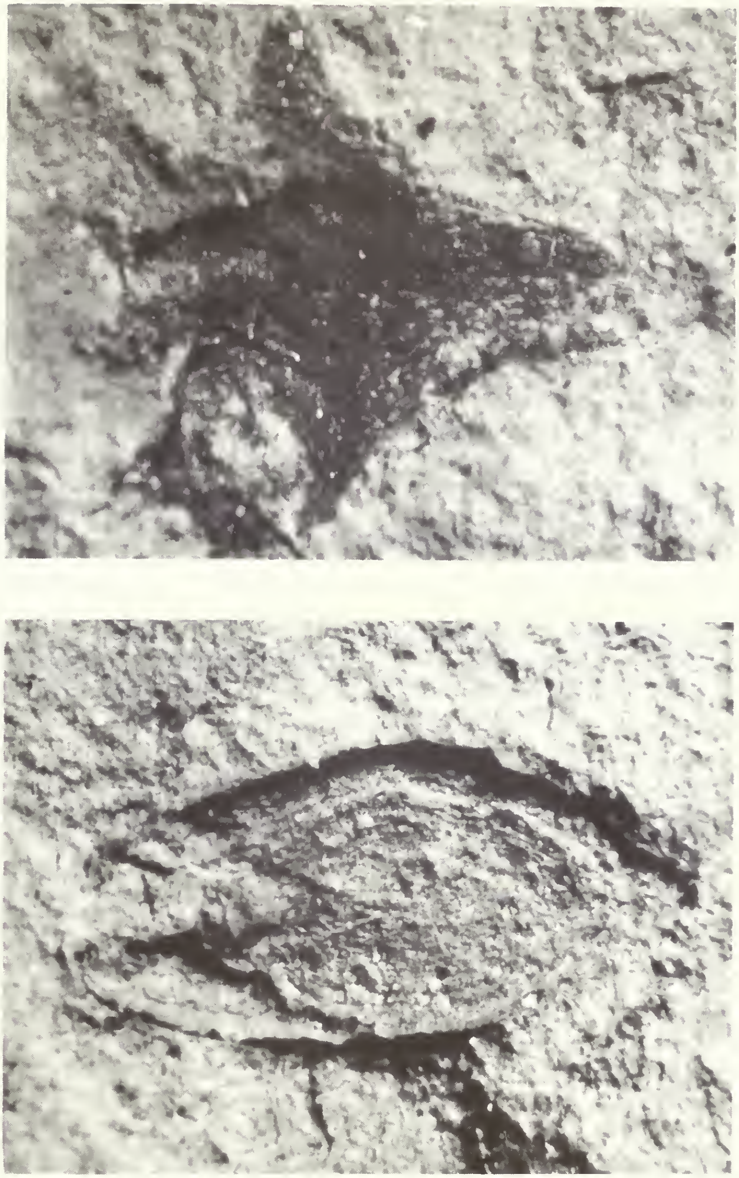


Fig. 1 *Carpolithus puddlebrookense* sp. nov., **holotype** V.60509a, × 15. I, integuments. S, salpinx. N, nucellus. P, prothallus.

ridges on the main body of the ovule which pass upwards into the free integuments. Two of the specimens possess short pedicels, 0·3 mm long, but none are attached to any other plant structure. Cellular details are not visible on any part of the ovules other than indications of longitudinal files of cells on the integument and nucellus. Two of the ovules appear to have a triangular mark projecting down from the apex of the nucellus, but this could be a preservation effect or the result of shearing strains as the rock was broken. These two ovules also show a marked depression which may indicate the area bounded by the lagenostome.

Compressions and casts of seeds are very difficult to assign to any genus with certainty. Crookall (1976) has reviewed these Carboniferous genera but persists in including many within the ill-defined genus *Carpolithus* Schlotheim, 1820. If the Drybrook specimens are to be given a name then it is within this genus that they are probably best included. The only species that are of comparable size are *C. ellipticus* Sternberg, *C. granulatus* Sternberg, *C. perpusillus* Lesquereux and *C. pseudosulcatus* Crookall, but they are all known only from the Westphalian and are themselves ill-defined. Crookall (1976) does describe his *Carpolithus* sp. A and sp. B from the Viséan but they are much larger than the present specimens. The Drybrook ovules are also similar in size to those included in *Lagenospermum* Nathorst, but they are more ovoid in shape and lack the longitudinal ribbing characteristically found on *Lagenospermum*.

The present ovules also show similarities to certain petrified ovules described by Long and other workers from the Calciferous Sandstone (Cementstone Group) of Berwickshire. They can be clearly included within the order Lagenostomales as outlined by Seward (1917) and modified by Long (1975). The possession of four integumental lobes, which are free only above the nucellus apex, and a distinct salpinx suggests that they could be included within the family Eurystomaceae. The closest genus of radially symmetrical ovules is *Eurystoma* Long 1960 emend. 1975 which has two species. *E. angulare* Long 1960 is the closer of the two to the present material, being comparable in size (4–8 mm long and 1–2·5 mm in maximum width) and in having four free apical lobes. The ovules, however, have much more prominent longitudinal keel-like ridges than those seen on the Drybrook specimens, giving them a squared outline when seen in transverse section. *E. burnense* Long 1975 is smaller (maximum size 5 × 3·5 mm) and is triangular in section with three very prominent wing-like ridges. Long has however shown that in the mature seed condition the keels decay or are eroded to give an almost circular outline in cross-section. The Drybrook ovules also differ from both these species in having less of a constriction of the level of division into free integumental lobes. However, it must be remembered that comparisons are being made between ovules which have been preserved in different ways. Longitudinal ridges and constrictions might easily have become less distinct during compression in the Drybrook shales.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Figs 2–3 *Carpolithus puddlebrookense* sp. nov. Fig. 2, **holotype** V.60509a, × 20. Fig. 3, associated plant organ, V.60509b, × 20.

These differences, however, hardly seem sufficient for generic distinction unless one decides that the different types of preservation preclude such a close comparison being made. This is clearly the crucial point of the identification. We are inclined to take the view here that it is not absolutely certain in this case, so the Drybrook specimens are described here as a new species under the name *Carpolithus puddlebrookense* sp. nov.

DIAGNOSIS. Oval radiospermic ovules. Length 4–8 mm, maximum diameter 2·5 mm. Integument 0·13 mm thick, fused to nucellus except above its apex where it is divided into four lobes 3 mm long. Diameter of salpinx about 0·3 mm.

HOLOTYPE. V.60509a. Figs 1, 2.

PARATYPES. V.60509b (Fig. 3), V.60510.

LOCALITY. Hazel Hill Quarry, Puddlebrook, Forest of Dean, Gloucestershire, England; National grid ref. SO 646184.

HORIZON. Drybrook Sandstone; lower Upper Viséan.

DISCUSSION. The decision to include the ovules in *Carpolithus* is supported by other evidence. Although the Drybrook specimens are very similar to *Eurystoma* on the evidence of their general morphology, the natural affinities of the two groups of seeds is possibly rather doubtful. Long has shown that his seeds were borne in a loose branching system interpreted as a primitive cupule and he suggested that the parent plants were of the frond type described as *Alcicornopteris* Kidston (Long 1969). No such branching cupules, nor fronds of the *Alcicornopteris* type, have been described from the Drybrook Sandstone and I have seen no suggestions of any while collecting there. Cupule-like structures, however, have been found and described as *Calathiops* sp. by Lele & Walton (1962 : pl. 21, figs 27–29) although the relationship of these to the seeds is as yet unknown. They are rather different from those cupules described by Long, being much more robust with the cupular lobes fused for nearly their whole length.

One other associated plant organ, on nos V.60509a and b (Fig. 3), may also have some affinity with the seeds. It has a short pedicel which is expanded into a broad head with four apical points. However, we have no firm suggestion to make about its structure or function.

Division **LYCOPHYTA**

Genus ***TOMIODENDRON*** Radczenko, 1956 emend. Meyen, 1972

Tomiodendron variabilis (Lele & Walton) comb. nov., emend.

Figs 4–14

DESCRIPTION. *Scutellocladus variabilis* was briefly described by Lele & Walton in 1962 as part of their study of the Drybrook Sandstone flora. Since then, however, many more detailed accounts have been published of other Lower Carboniferous lycophytes, so this species warrants critical re-investigation. Lele & Walton's material therefore has been re-examined together with many new specimens from the same locality.

The majority of stem fragments are preserved only as impressions and very few retain any fragments of compressed plant material. The stems at first sight appear to be quite varied, but careful study revealed them to be all of the same general form. It was the splitting of the rock that controlled how the stem was exposed in many different ways. There are theoretically many surfaces that may be visible as a result of rock splitting along different planes and most can be seen on the various specimens available to us (Fig. 4). The stems are unbranched, except for a few that dichotomize, are up to 13 cm long and range in width between 0·2 and 2 cm. Leaves can be clearly seen attached to some of the stems (Fig. 6). They are spirally arranged, about 1 cm long and 2 mm broad, falcate in outline with acutely pointed apices. Many show a slight central ridge which we interpret as a leaf vein.

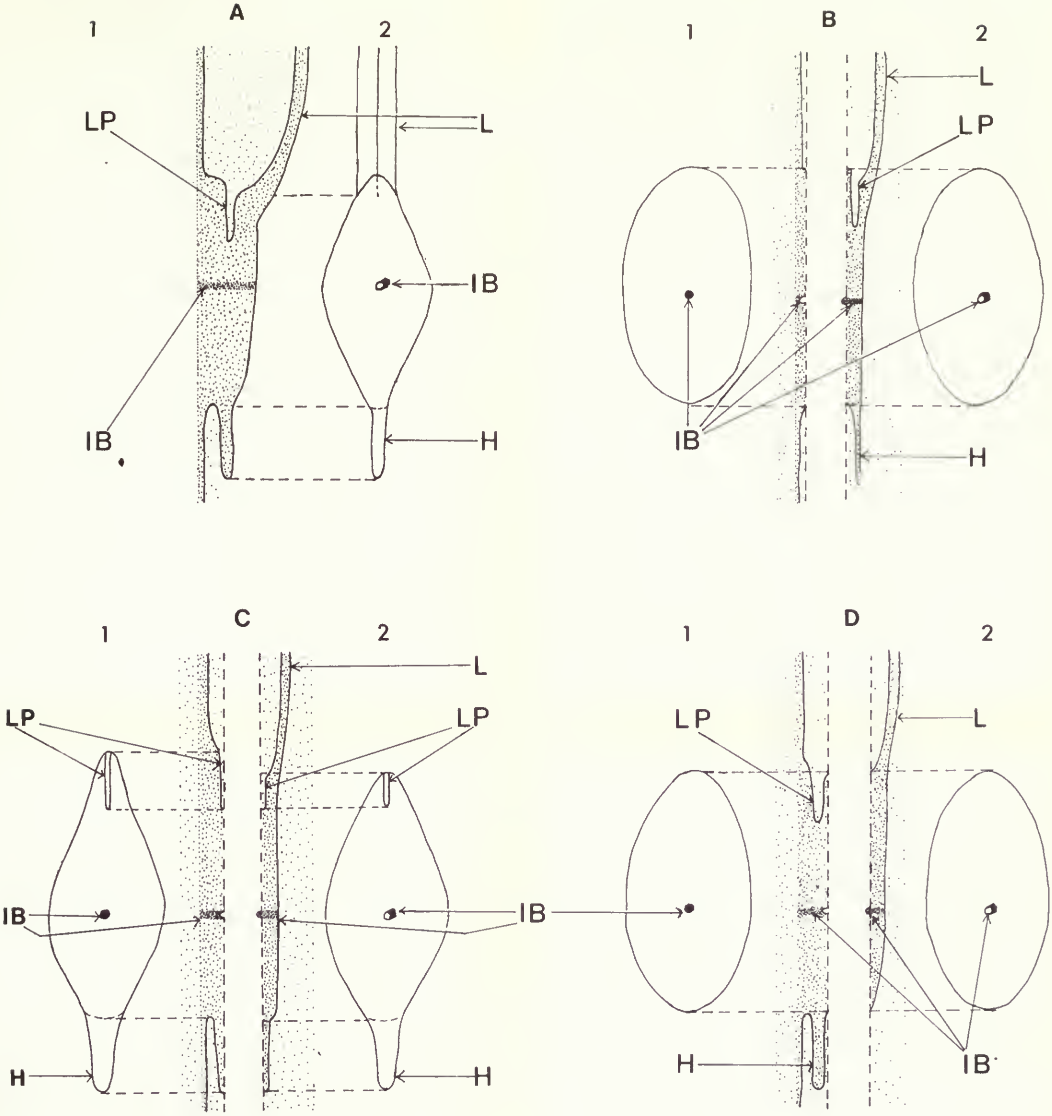

Fig. 4 *Tomiodendron.* Diagram to illustrate inter-relationships between preservation and fragmentation. Leaf cushions are illustrated in different aspects of exposure. The different preservation polymorphs are related to the ways that the matrices fractured to reveal the stems. Example A shows a situation where the fracture plane occurs at the surface of the compression, whereas B, C and D are cases where the fracture lines have sheared through the compression. Very little evidence is ever seen of leaf laminae, but heels are more often exposed (as in A2, C1 and C2). Ligule pits are also only sometimes seen (as in C1 and C2). The nature of the marks left by the infrafoliar bladders are consistent; they always collapsed inwards during preservation. They are illustrated here as infrafoliar projections on the right of the pairs, and as depressions on the left of the pairs of preservation polymorphs. In each example the central shaded part is an imaginary section, and the shapes at either side show the appearance of the fracture surface on the exposed rock surface. H — heel, IB — infrafoliar bladder, L — leaf, LP — ligule pit.

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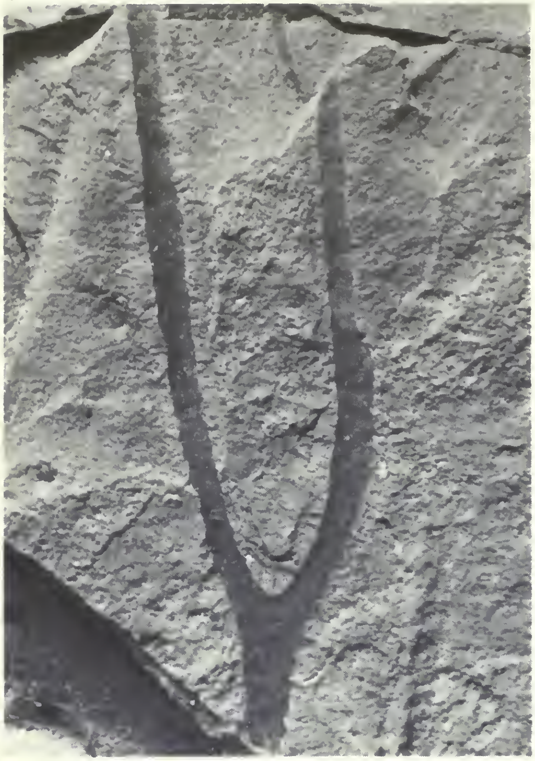

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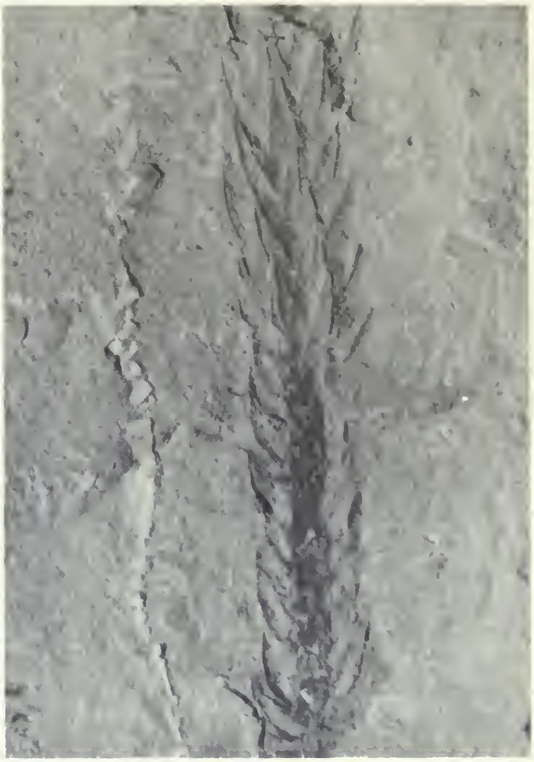

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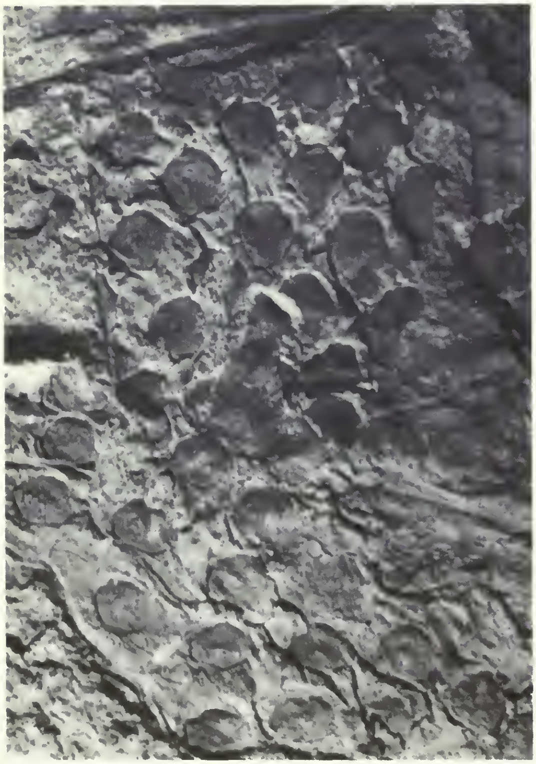

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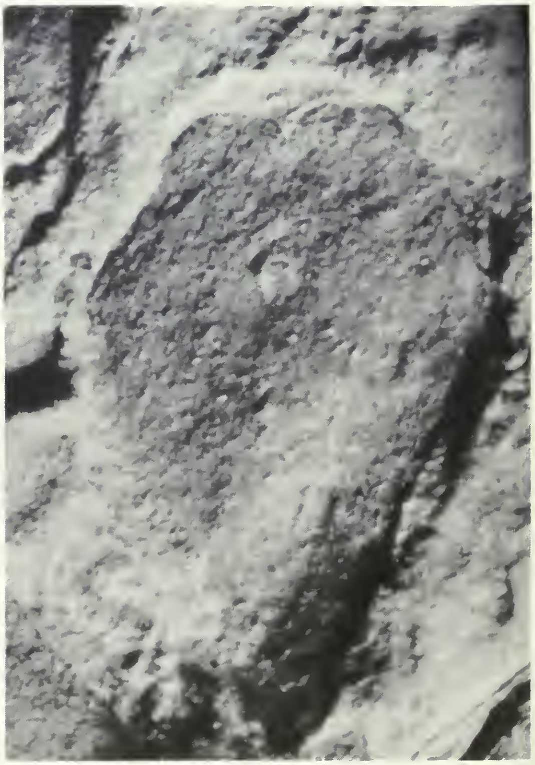

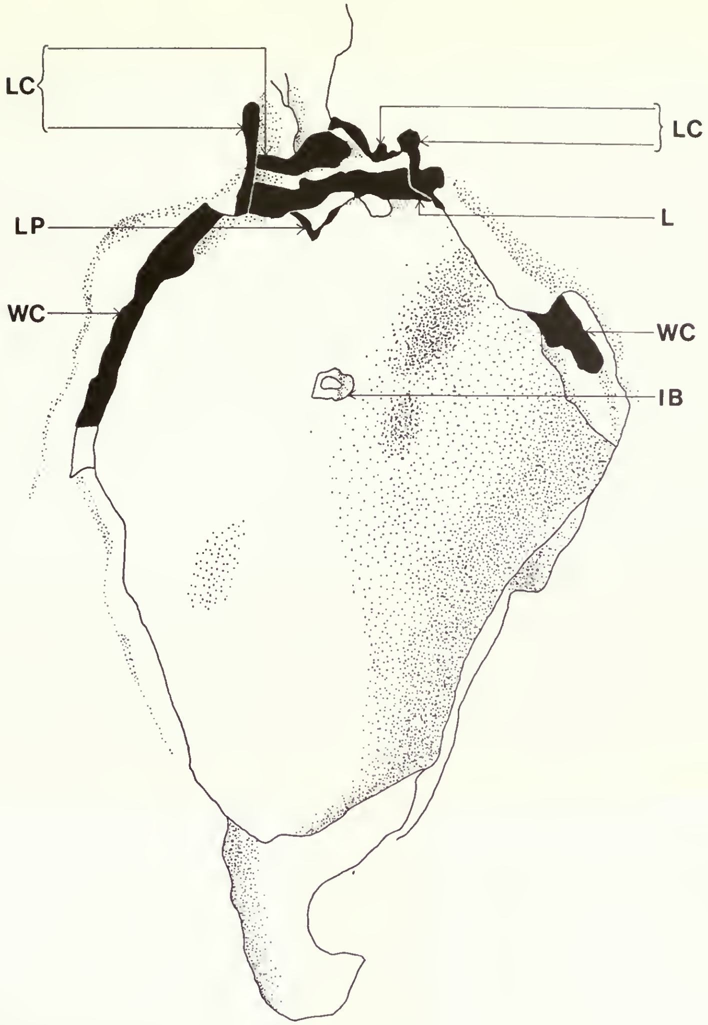

Fig. 9 *Tomiodendron variabilis.* Leaf cushion impression showing remains of leaf, wing, and ligule pit compression material. The upper angle of the leaf cushion and the base of the leaf lamina were uncovered by degaging. This specimen exhibits the type of fracture surface shown in Fig. 4, C2. IB, infrafoliar bladder. LC, compression of apical portion of leaf cushion. L, leaf lamina compression. LP, ligule pit. WC, wing compression. V.60346, ×25.

Many stems appear to have lost their leaves, instead having ovoid to rhomboidal scar-like outlines (Fig. 5). However, we interpret these as impressions of swollen leaf bases and believe that the leaf laminae were either not preserved during fossilization or were mechanically separated and lost during the splitting of the rock.

The swollen leaf bases can be described as leaf cushions for the reason given below. The ovoid leaf cushions are generally found on twigs less than 1 cm broad, are about 2 × 1 mm

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Figs 5–8 *Tomiodendron variabilis* (Lele & Walton) comb. nov. Fig. 5, leafless stem showing dichotomy, V.60223, ×2. Fig. 6, leafy stem, V.60350, ×2. Fig. 7, stem with rhomboid leaf cushions (compare with Fig. 4, A2 and C2), overlain by one with oval leaf cushions (compare with Fig. 4, A1, B1 and/or D1), V.60346, × 4. Fig. 8, rhomboid leaf cushion with ligule pit cast (enlargement of Fig. 7), V.60346, ×20.

to 2·75 × 1·5 mm in size and separated by about 0·5 mm to 1·5 mm of stem surface (Fig. 7). The virtually symmetrical rhomboidal cushion outlines are up to 5 × 3·5 mm in size and about 0·5 mm to 1·5 mm apart (Figs 7, 8). Changes in density and dimensions of leaf cushions do however occur on some stems. Sunken leaf cushions, which we interpret as impressions of the outer surface of the stem, often have carbonaceous compression material around their edges disappearing into the matrix. Careful degaging reveals this to represent lateral extensions of the cushions similar to the wings described in *Tomiodendron* sp. and *Angarodendron leclerquianus* by Meyen (1976). Some of the sunken cushions also have carbonaceous compression material extending into the matrix at their lower angles, while others show extensions of the cushion depressions into short shallow grooves. From this evidence we conclude that the cushions had small heels.

Ligule pit casts are present in the upper angles of many leaf cushion impressions (Figs 8, 12), although their presence seems to depend on the way the rock split rather than on their actual preservation. The pit casts are roughly triangular in outline, with apertures 0·5 mm wide, and varying in length between 0·2 and 0·33 mm. Leaf laminae can usually be seen as lines of compression material running across the leaf cushion immediately above the apertures of the ligule pits (Fig. 9).

Some stem impressions are preserved in such a way that their leaf cushions are shown to extend into a rounded apex above the line of attachment of the leaf lamina. This subapical attachment of the leaf lamina leads us to describe the swollen leaf bases as leaf cushions even though leaf abscission does not occur. If the lamina was attached apically to the swollen leaf bases making the leaf attachment decurrent it would be more suitable to call them leaf bases. Many leaf cushions have a single, circular depression or projection which again needs to be interpreted in the knowledge of the type of stem preservation. Projecting cushions seen as in

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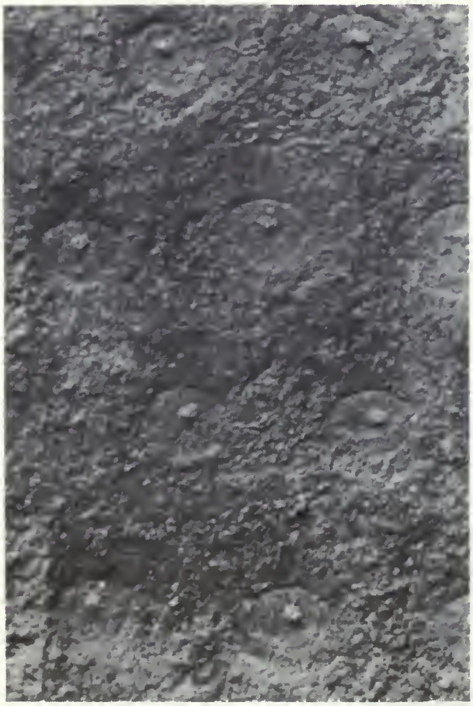

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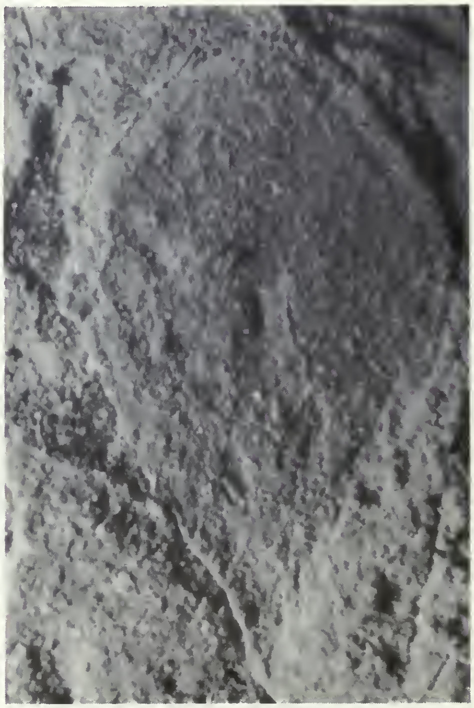

Figs 10–11 *Tomiodendron variabilis*, infrafoliar bladders. Fig. 10, leaf cushions with infrafoliar projections (compare with Fig. 4, B2 and D2), V.60344, ×10. Fig. 11, leaf cushion with infrafoliar depression (compare with Fig. 4, C2), V.60346, ×20.

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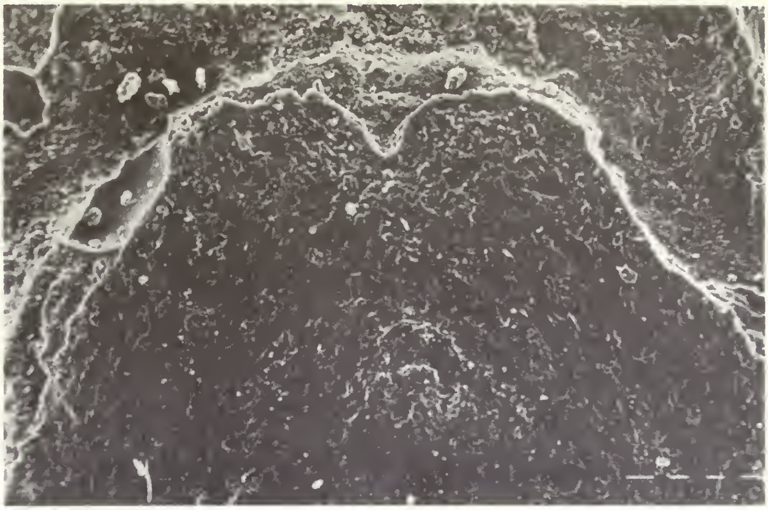

Fig. 12 *Tomiodendron variabilis*. Leaf cushion and ligule pit cellular detail (displayed using scanning electron microscope), V.60346, ×30.

life have depressions, while cushion impressions have projections. Similar, but larger, structures have been described as infrafoliar bladders in *Tomiodendron* by Meyen (1976) (Figs 10, 11).

Cellular detail can be seen on some leaf cushion surfaces using a binocular microscope, so latex moulds were prepared for observation with the scanning electron microscope. Cells about 30 × 15 μm in size were visible along the axis of the leaf cushion (Fig. 12). No stomata were seen but it should be remembered that the cellular detail was generally poor. Cuticle was also prepared from small fragments of compression taken from intercushion areas of a stem. All the cells were similar, being polygonal, slightly elongated towards the cushions and measuring about 30–40 × 15–20 μm with anticlinal walls 10 μm thick. No stomata were visible (Figs 13, 14).

COMPARISON. The Puddlebrook species was clearly a ligulate lycophyte stem although we have no idea of the size to which the plants grew. Many other genera of Lower Carboniferous lycophytes are similarly only imperfectly known, although many exhibit features closely comparable with some of our stems. Therefore we will confine our attention to those ligulate stems which are of comparable size. They are *Tomiodendron* Radczenko emend. Meyen 1972, *Angarodendron* Zalessky emend. Meyen 1976, *Ursodendron* Radczenko emend. Meyen 1972, and *Eskdalia* Kidston emend. Thomas 1968.

Russian Lower Carboniferous species of *Tomiodendron* have been described by Meyen (1972, 1976) and Gorelova (1978). Their descriptions of the leaf cushions lead to the conclusion that the genus *Scutellocladus* may be regarded as synonymous with *Tomiodendron*. The British specimens are, however, sufficiently different from all the Russian ones to be kept as a separate species and named *Tomiodendron variabilis* (Lele & Walton) comb. nov. (Table 1).

Angarodendron obrutschevii Zalessky emend. Meyen was originally diagnosed as eligulate, as was *T. variabilis*, although it is now known to be ligulate. *Angarodendron* did, however, shed its leaves and also has much larger infrafoliar bladders that sometimes occupy more than half the cushion width.

Ursodendron is very similar in its leaf cushion morphology but always has its cushions in

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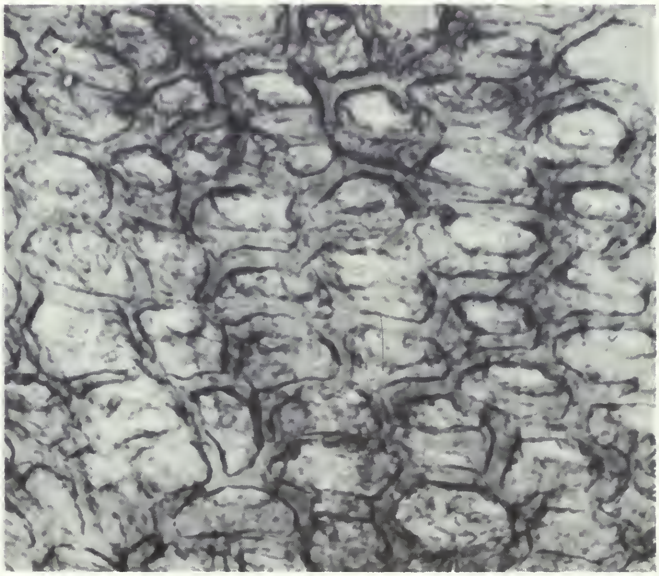

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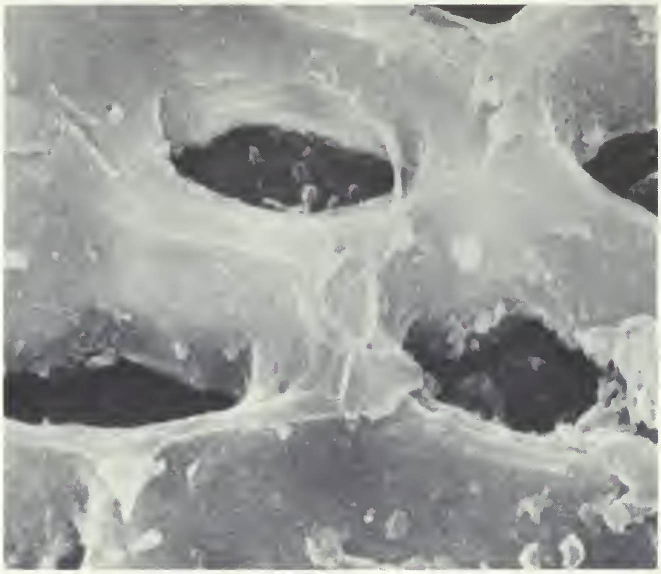

Figs 13–14 *Tomiodendron variabilis*, cuticular material. Fig. 13, stem cuticle from V.42519, ×500. Fig. 14, stem cuticle (view from inner side with scanning electron microscope) of V.42519, ×1500.

Table 1 Comparison of characters of *Tomiodendron variabilis* (Lele & Walton) comb. nov. with described Russian species of *Tomiodendron*.

Species	Phyllotaxy	Shape of leaf cushions	Size of leaf cushions	Infrafoliar bladder	Intercushion distance	Intercushion ornamentation
T. ostrogianum Zalessky, emend. Meyen	Regular orthostichies. Crossing parastichies at 80°–85°	Rhomboidal	7–15 mm long 2–5 mm wide	Linear, 1 mm wide	0·5–2 mm	Striated
T. kemeroviense Chaclov, emend. Meyen	No orthostichies	Lanceolate or narrow elliptical	8–16 mm long 2·5–4 mm wide	Longitudinal fold, 6 mm long, 1·5 mm wide	< 5 mm	Wrinkled
T. asiaticum Zalessky, emend. Meyen	No orthostichies	Oval	7 mm long 3·5 mm wide	Longitudinal fold	< 5 mm	Smooth
T. tetragonum Gorelova	No orthostichies. Crossing parastichies at 20°–40°	Rhomboidal to square	4–7 mm long and wide	–	2–4 mm	Smooth or slightly wrinkled
T. regulare Meyen	Vertical orthostichies	Rhomboidal to oval	7 mm long 2·5–4 mm wide	Central, 0·5–0·7 mm wide	3–4 mm	Finely striated
T. variabilis (Lele & Walton), emend. herein	No orthostichies. Crossing parastichies at 20°–40°	Rhomboidal to oval	Rhomboidal: 5 × 3·5 mm Oval: 2–2·75 mm long 1–1·75 mm wide	Circular, 0·02–0·05 mm wide	0·5–1·5 mm	Smooth

horizontal rows. It also has many stomata on its leaf cushions whereas *Tomiodendron* seems to have none.

Eskdalia has been described as having leaf abscission by Chaloner (1967) and Thomas (1968) but it is now thought to have had persistent leaves (Meyen & Thomas, unpublished). The leaf laminae in *Eskdalia*, however, seem to arise from almost the extreme upper edge of the oval leaf cushions, and the cushions themselves have no infrafoliar bladders.

EMENDED DIAGNOSIS. Stems up to 2 cm broad. Leaves falcate with acute apices, about 1 cm long, attached to ovoidal-rhomboidal leaf cushions measuring up to 5 × 3·5 mm. Ligule pits triangular up to 0·33 mm long with apertures of 0·5 mm. Infrafoliar bladders central and less than one tenth of the maximum width of cushions. Cushion epidermal cells about 30 × 15 μm in size, longitudinally elongated. Stem epidermal cells measuring 30–40 × 15–20 μm, elongated towards leaf cushions.

LECTOTYPE. V.42433, herein selected. Lele & Walton 1962 : pl. 19, figs 1, 2.

LOCALITY. Hazel Hill Quarry, Puddlebrook, Forest of Dean, Gloucestershire, England; National grid ref. SO 646184.

HORIZON. Drybrook Sandstone; lower Upper Viséan.

Acknowledgement

The photographs of the specimens were taken with a Wild M8 microscope whose purchase was financed by a grant from the Royal Society. This we gratefully acknowledge.

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Bintoniella brodiei Handlirsch (Orthoptera) from the Lower Lias of the English Channel, with a review of British bintoniellid fossils

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Synopsis

The Bintoniellidae is an extinct family of Mesozoic Orthoptera Ensifera. Fifty-three specimens of *Bintoniella brodiei* Handlirsch (mainly wings) from seven localities in southern England and the English Channel were examined. These specimens are from four different zones of marine Lower Lias and Rhaetian deposits (Lower Jurassic and Upper Triassic). It is concluded that *brodiei* is sexually dimorphic by analogy with recent bush-crickets (Tettigoniidae). The palaeoecology of the fossils is discussed.

Introduction

During the study of fossil insects from the British Jurassic a specimen was received from the Institute of Geological Sciences which had been found in a core of Lower Lias drilled under some 78–80 m of water (see p. 146) below the surface of the English Channel. This wing (Figs 1, 2) was clearly similar to some of the Orthoptera amongst the fossils already being studied. Because of the interest of the new locality, a more detailed study of these related Orthoptera was undertaken. They had not been included in Zeuner's monograph of the Orthoptera Ensifera (1939) because he regarded them as part of a 'side branch from the phylogenetic line' (Sharov 1968). Material from all the British Lower Jurassic in the collections of the Institute of Geological Sciences, British Museum (Natural History) (BM(NH)) and Bristol Museum has been examined, although no specimens of Bintoniellidae were found in the latter. Over fifty specimens were found, mostly wings but with some body structures, which probably represent the same species of *Bintoniella* and are conspecific with the specimen from the English Channel.

Systematics

Family **BINTONIELLIDAE** Handlirsch, 1939

The family Bintoniellidae was proposed by Handlirsch (1939) based on the drawing of an insect wing by Brodie in 1845 under the title of a 'Neuropterous insect allied to *Chauliodes*'. Brodie's figure was copied by Handlirsch who also proposed a new generic and specific name for the fossil. There is no evidence that Handlirsch examined the original specimen. Subsequently Sharov (1968) redefined the family and genus based on new material from the Lower Trias of the USSR and some specimens from the Lower Jurassic of Britain (incorrectly recorded by Sharov as Upper Trias). Sharov (1968) figured two specimens (In.10464, In.10583) which are both from the type locality of the species in Warwickshire and are also in the BM(NH) collection.

Genus ***BINTONIELLA*** Handlirsch, 1939

TYPE SPECIES. By monotypy, *Bintoniella brodiei* Handlirsch (1939 : 55).

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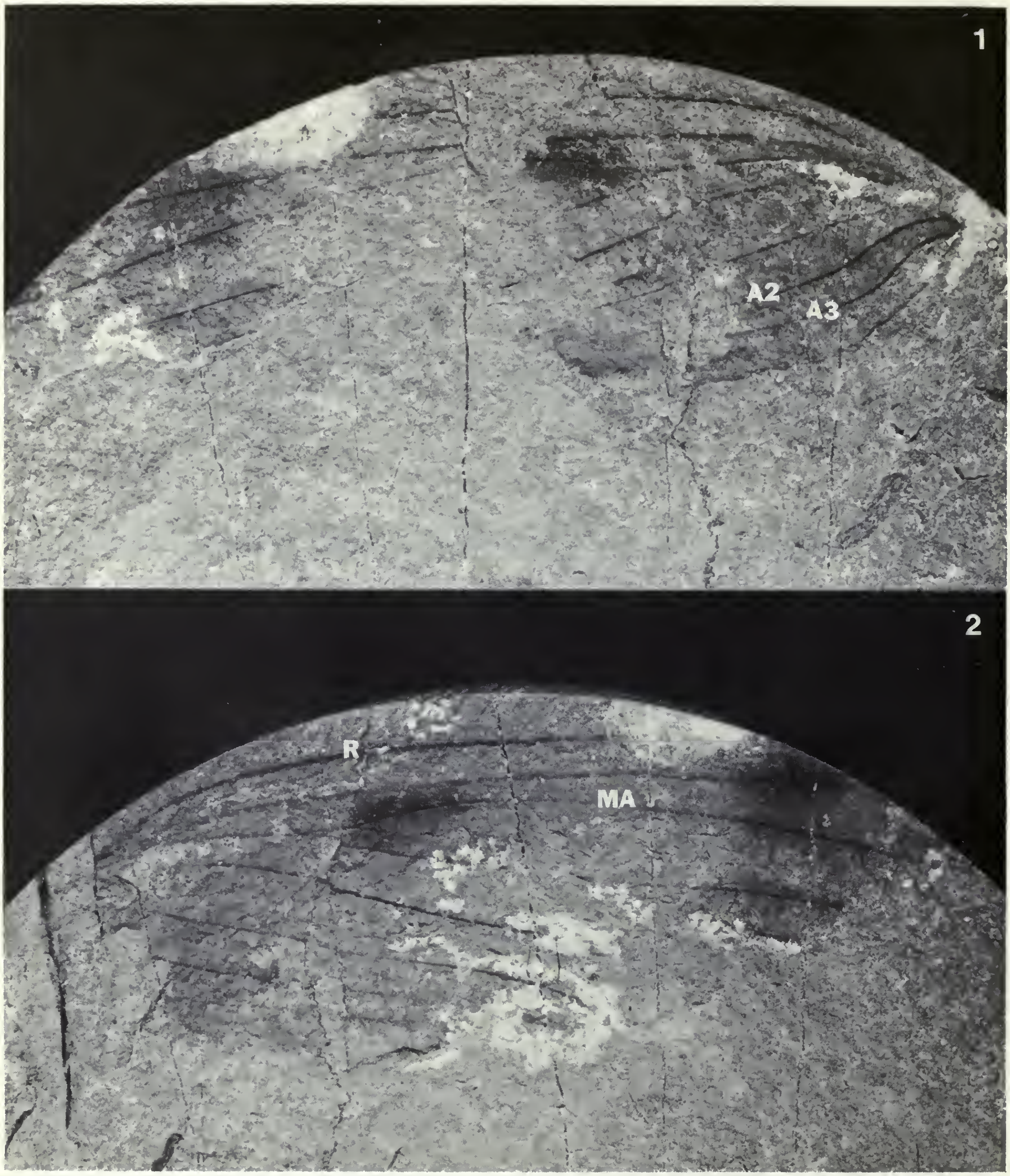


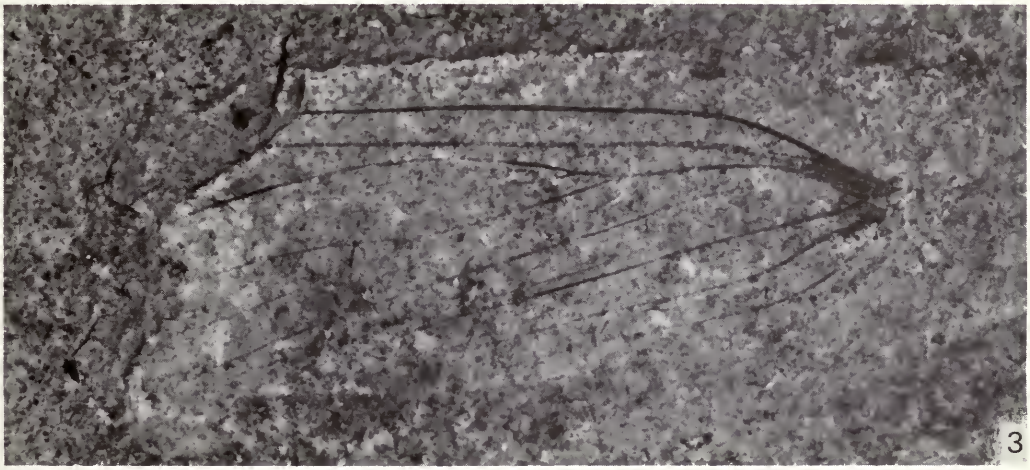
Figs 1, 2 *Bintoniella brodiei* Handlirsch. Fig. 1, male, forewing. English Channel, *c.* 67 km south of Plymouth. Lower Jurassic, Rotiforme Subzone of Bucklandi Zone, Lower Lias. Institute of Geological Sciences, C.S.E. 6178. Length 33 mm, width 11 mm. Fig. 2, the same (counterpart); C.S.E. 6179.

Handlirsch characterized the family and genus by the large precostal area at the base of the forewing (Fig. 6). Sharov (1968) also used this character and pointed out that the number of branches of MP and CuA in the British specimens is reduced; he considered CuA as a cross vein which joins MP near the base. While this is true of many specimens, in some CuA may separate off after fusing with MA for a short distance and run separately to the wing margin. Sharov related the Bintoniellidae to the Vitimiidae, both of which he placed in the Oedischiidea, a superfamily of the Orthoptera Ensifera.

Bintoniella brodiei Handlirsch, 1939
Figs 1–6

1845 'allied to *Chauliodes*'; Brodie : 102; pl. 10, fig. 6.
1939 *Bintoniella brodiei* Handlirsch : 55.
1968 *Bintoniella brodiei* Handlirsch; Sharov : 41, fig. 16.

HOLOTYPE. Male. Lower Lias, Binton, Warwickshire; *ex* Brodie coll. BM(NH) In.10463 (Fig. 3). This is one of the larger specimens from the Planorbis Zone at Binton. It has only a lightly sclerotized membrane which has not been preserved over most of the fossil.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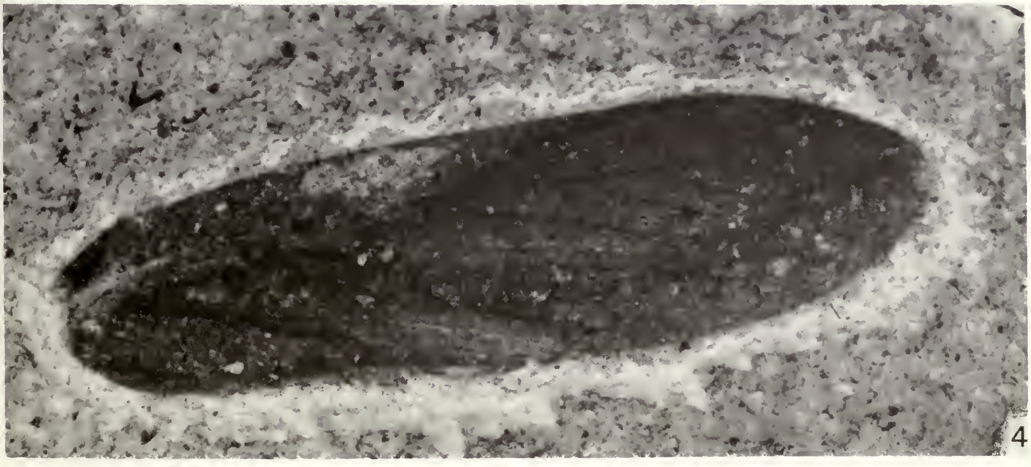
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Figs 3, 4 *Bintoniella brodiei* Handlirsch. Planorbis Zone, Lower Jurassic, Binton, Warwickshire. Fig. 3, holotype male, forewing. BM(NH) In.10463. Length 31 mm, width 12 mm. Fig. 4, female, forewing. BM(NH) In.6784. Length 27 mm, width 9·5 mm.

OTHER MATERIAL. All specimens except the last are in the BM(NH).

Binton, Warwickshire: Males, In.6652, In.6661, In.6675, In.6766, In.6783, In.10578, In.10932, In.11080. Females; In.3375, In.3383, In.6656 (Fig. 6), In.6770, In.6780, In.6784 (Fig. 4), In.10464 (Sharov 1968 : 41, fig. 16), In.10479, In.10585, In.10933, In.10935. Sex indet.; In.3384, In.6654, In.6659, In.6773, In.10463.

Brown's Wood, Warwickshire: Hind wing; In.10588. Female; In.10616. Male (?); In.10592.

Stratford-on-Avon, Warwickshire: Sex indet.; In.6799, In.10475, In.10668.

Grafton, Warwickshire: Females; In.6799, In.10495, In.11217.

Strensham, Worcestershire (Rhaetian, see Whalley, in press): Males; In.10439, In.10447, In.10457, In.10530, In.10538, In.10539, In.10542, In.11109, In.11112, In.11237. Females; In.10443, In.10554 (Fig. 5). Sex indet.; In.10446, In.10532.

Climbers (no other data, Warwickshire ?): Female; In.6790.

Lower Lias, England (no other data): Females; In.15002, In.15012.

Western English Channel *c.* 67 km south of Plymouth (78–80 m below sea level) at depth 17·72 m: Male part and counterpart; C.S.E. 6178+6179 (Figs 1, 2). This is from the Rotiforme Subzone of the Bucklandi Zone, Lower Lias. In the Institute of Geological Sciences.

All the specimens examined fall clearly into the two size groups mentioned below and are regarded as males and females of one species, *B. brodiei*.

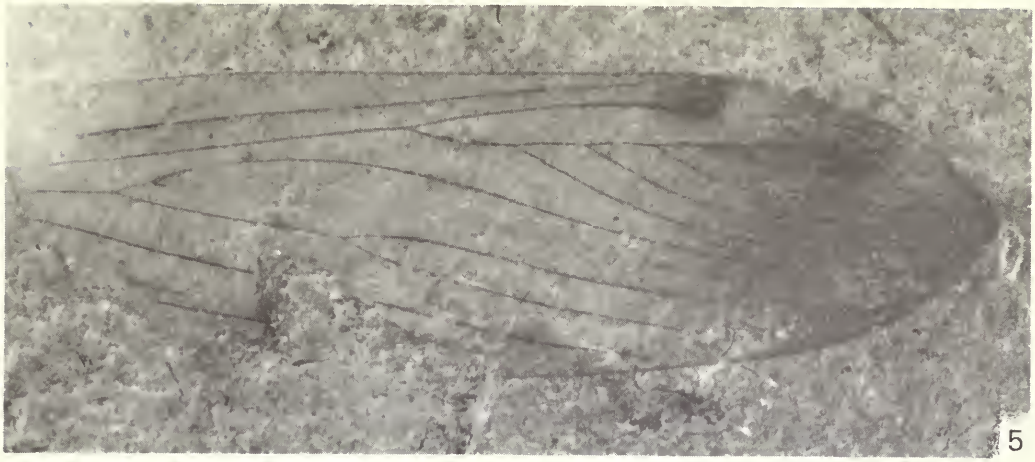
DESCRIPTION. Where preserved, the precostal area is large (Fig. 6) and the subcostal vein reaches well towards the wing tip. There are strong, regular cross-veins between this and the radial vein. Rs separates in about the middle of the wing and forms four or sometimes five branches to the wing margin. The characteristic median vein is described below while Cu_1 is apparently fused with MP, separating in a few specimens at the wing margin. Of the three anal veins, A2 and A3 form a distinctive and highly characteristic loop at the base of the wing where they join. This shows clearly in many of the specimens examined.

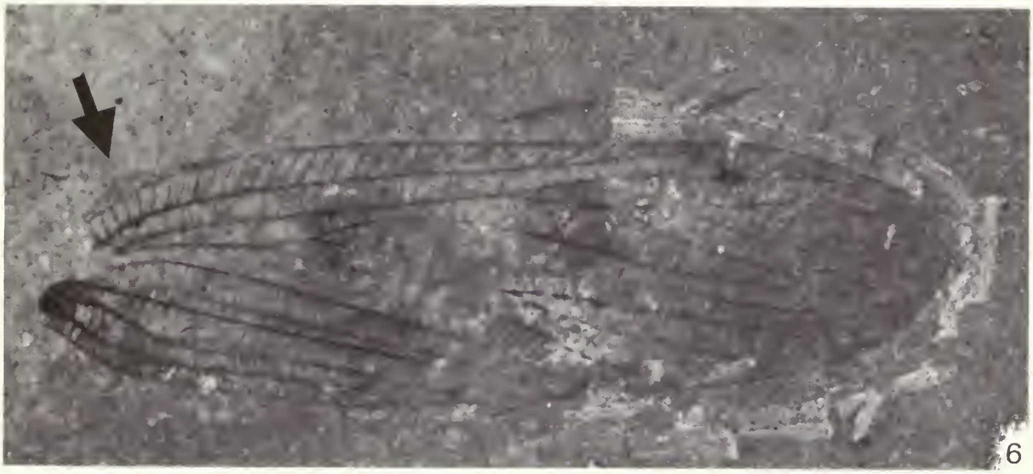
DISCUSSION. Sharov (1968) illustrated the hind wing of this species, which shows the characteristic median branching of the forewing, lacks the precostal area and has a greatly enlarged anal fan. The forewing from the English Channel (Figs 1, 2) is incomplete but clearly shows the median vein branches and the anal loop. It evidently had a more curved outline and was one of the larger specimens here regarded as the males of *B. brodiei*.

Only the wing impressions of bintoniellids were available to Sharov and earlier workers but some parts of the body have now been found. This shows a typical 'bush-cricket' type of body-shape and a strongly spined hind tibia on which the spines are arranged in two rows. The tarsal segments were also lightly spined. The antennae have not been found but like other bush-crickets were almost certainly long and filamentous.

The large size and delicate venation of the precostal area (Fig. 6) shows well in many of the specimens examined: see Ragge (1955). The most characteristic feature is, however, the triple branching of the median veins. There is some variation in the number of divisions of the anterior radial vein which usually has four main branches but in some specimens a fifth branch is present. Apart from these small differences, the venation of the specimens is very constant.

DIMORPHISM. The most striking feature of the material examined is the two sizes of wings with similar venation but with differences in the degree of sclerotization of the wing membrane (compare Figs 1–3 with Figs 4–6). The complete wings of the larger specimens are 34–45 mm long × 10–12 mm wide. These specimens show very little trace of the wing membrane, which suggests that it was probably lightly sclerotized. The smaller wings are 25–30 mm × 7·8–9·2 mm and have the wing membrane in most cases clearly visible on the matrix as a black area, suggesting that, in life, these wings were more heavily sclerotized. The outline shapes of the wings differ, with the smaller, more sclerotized wings having more or less parallel costal and hind margins, while the larger ones have more curved margins. Although it is possible to consider them as two distinct species with similar venation, I think





Figs 5, 6 *Bintoniella brodiei* Handlirsch. Fig. 5, female, forewing. Rhaetic, Strensham, Worcestershire. BM(NH) In.10554. Length 26·5 mm, width 9·0 mm. Fig. 6, female, forewing, precostal area arrowed. Planorbis Zone, Lower Jurassic, Binton, Warwickshire. BM(NH) In.6656. Length 28·5 mm, width 9·0 mm.

that this dimorphism represents a sexual difference within one species. Ragge (1960) commented on sexual dimorphism in the Acrometopae (Orthoptera, Tettigoniidae) and particularly in the genus *Horatosphaga* Schaum., in which the males have large wings which are more lightly sclerotized than those of the females. The shape of the wings is also different, the males having a more curved margin while female wings are straighter and more slender (Fig. 7). Amongst the specimens of *B. brodiei* studied, there are twenty males and twenty females while twelve specimens are too incomplete to sex.

Distribution and habitat

Although insect fossils are common in Lower Jurassic deposits from Dorset, no specimens of Bintoniellidae have been found and it would appear that the family was not represented in the area from which they were derived. The Dorset fossils include many ammonites together with the insects (Zeuner 1962), which suggests a coastal derivation. A possible ecological

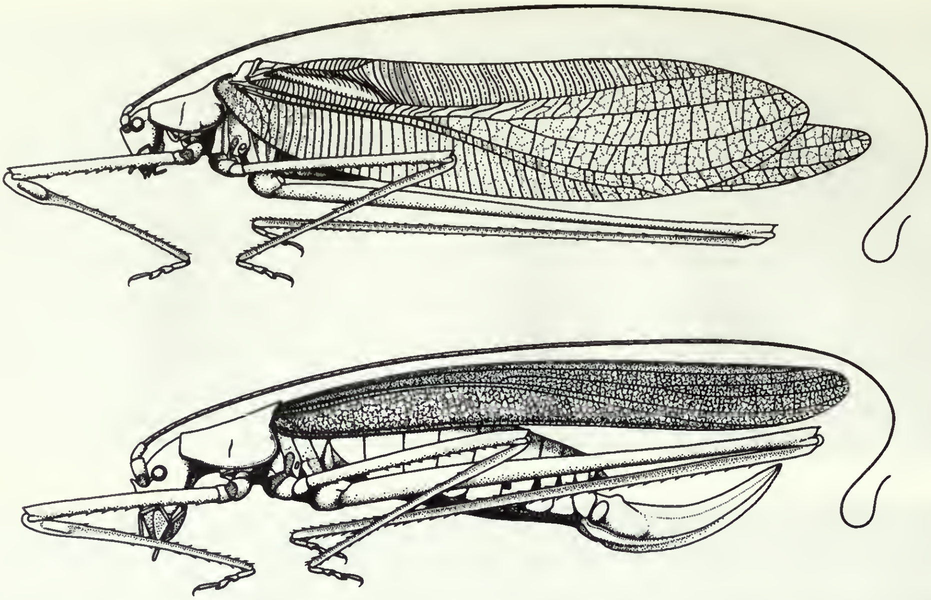


Fig. 7 *Horatosphaga* sp. (Orthoptera: Tettigoniidae). Recent bush-cricket, male above, female below, showing sexual dimorphism in shape and texture of forewing (Illustration from Ragge, 1960 : 275, fig. 1).

difference is thus indicated, as well as the stratigraphic differences which exist between Dorset and the Midlands. The Binton beds are Planorbis Zone and those of Strensham are Rhaetian, older than the Bucklandi Zone of the Channel, while the Obtusum Zone of Dorset is stratigraphically the youngest.

An interesting problem raised by the discovery of the specimen from the English Channel is its origin. Was it there because it flew out to sea and was trapped in marine mud, or was the core taken from close to the Jurassic shoreline? Generally the modern representatives of the long-horned bush-crickets are not long-distance migrants. Many are relatively solitary in their habits although some of the tropical species swarm at certain times of the year. If *B. brodiei* is dimorphic and broadly comparable in this respect to Recent *Horatosphaga* (see Ragge, 1960) then the females may even have had reduced hind wings and been unable to fly. Examination of the two specimens in which fore and hind wings are associated shows them both to be the larger (male) insect, which therefore was presumably able to fly. There is no direct evidence yet that female bintoniellids were unable to fly. The specimen from the Channel is also a large, male, specimen.

The bush-crickets are stout and substantial, and less prone to the effects of strong winds than many other insects. On balance, I consider the Channel specimen was either brought down in a river and deposited at the site where it was found, or that the species actually lived nearby. The latter would imply that during the Lower Jurassic the English Channel area, in or near where the fossil was found, was covered in trees and other vegetation and ecologically similar to the area where *Bintoniella* was abundant in the Jurassic, at Binton, Warwickshire.

Acknowledgements

I am grateful to Dr H. Ivimey Cook, Institute of Geological Sciences, for drawing my attention to the specimen from the English Channel and for allowing me to study it. Dr D. R. Ragge, British Museum (Natural History), allowed me to use his original drawing of the bush-crickets and saw the draft of the manuscript. Mr E. A. Jarzembowski, BM(NH), also read the manuscript; to both I offer my thanks.

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Uraloporella Korde from the Lower Carboniferous of South Wales

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Synopsis

Uraloporella Korde, 1950 is recorded for the first time in Britain. It occurs in the Lower Carboniferous Llanelly Formation (Arundian?) of south Wales. A plot of its dimensions compares well with that of *Uraloporella variabilis*. The taxonomy of this problematical microfossil is reviewed and aspects of its occurrence and environmental distribution are discussed.

Introduction

The fossils described here were discovered during the course of examining material from the Lower Carboniferous Llanelly Formation of south Wales (see Wright 1981*a*), a thin peritidal and alluvial unit of probable Arundian age (Institute of Geological Sciences 1976), which outcrops along the north-east part of the South Wales Coalfield (George 1954, Wright 1981*a*).

The Llanelly Formation was originally named the Calcite Mudstone Group by George (1954) but was later renamed the Llanelly Formation (George *et al.* 1976). George (1954) named the upper limestone part of the unit the *Linoproductus* Oolite, but specimens of that brachiopod are rare and the oolite was renamed the Penllwyn Oolite Member by Wright (1981*a*). George also recognized a persistent, coarsely bioclastic unit at the base of the oolite which he named the *Composita* Bed. The brachiopod *Composita* is rarely found in this bed but the problematical tubiform microfossil *Uraloporella* Korde is often abundant, locally making up 40% of all allochems, hence the bed has been renamed the *Uraloporella* Bed (Wright 1981*a*).

The *Uraloporella* Bed is a buff-weathering bioclastic limestone which varies from a few cm to 50 cm thick. It is a moderately to poorly sorted, often coarse-grained bioclastic grainstone containing intraclasts, peloids, quartz sand and fragments of brachiopods, crinoids, foraminifera, ostracods and the dasycladacean alga *Koninckopora*, as well as *Uraloporella*. This bed, traceable throughout the outcrop of the Llanelly Formation, has been interpreted as an open marine transgressive 'surf zone' deposit and further details of its composition and detailed locality information can be found in Wright (1981*a*).

Systematic description

MICROPROBLEMATICUM, *incertae sedis*

Uraloporella variabilis Korde, 1950

Figs 1, 2

The skeletal remains consist of small, straight cylindrical tubes, up to 1 mm long, 63–400 μm in diameter and with thick calcareous walls 11–71 μm in thickness (see Figs 1, 2). Wall thickness increases with increasing tube diameter (Fig. 3). The wall is micritic to fibrous in

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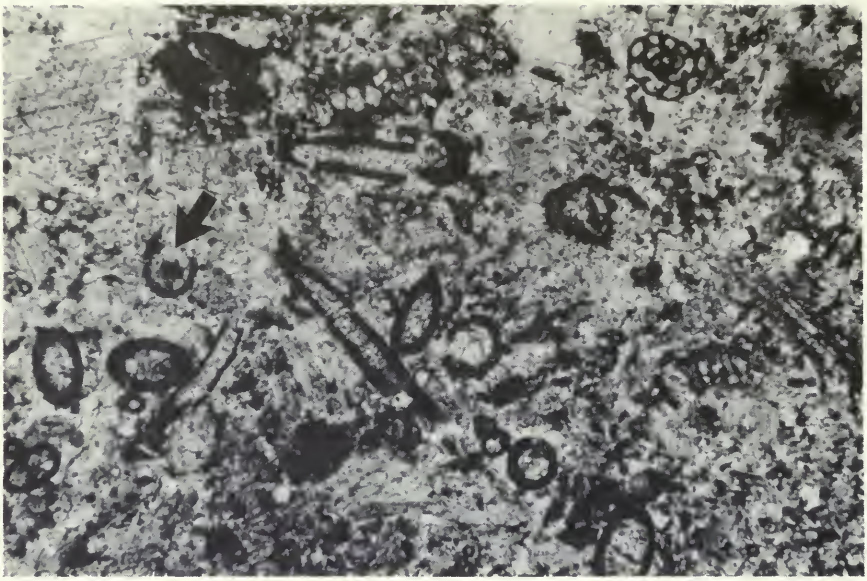

Fig. 1 *Uraloporella*, transverse and longitudinal sections. Note the patchy recrystallization of walls (arrowed). *Uraloporella* Bed, Clydach Halt Lime Works (National Grid ref. SO 2342 1261; Wright 1981*a* : 352). British Museum (Natural History) Dept Palaeontology, reg. no. V.60809a. Field of view is 4 mm wide.

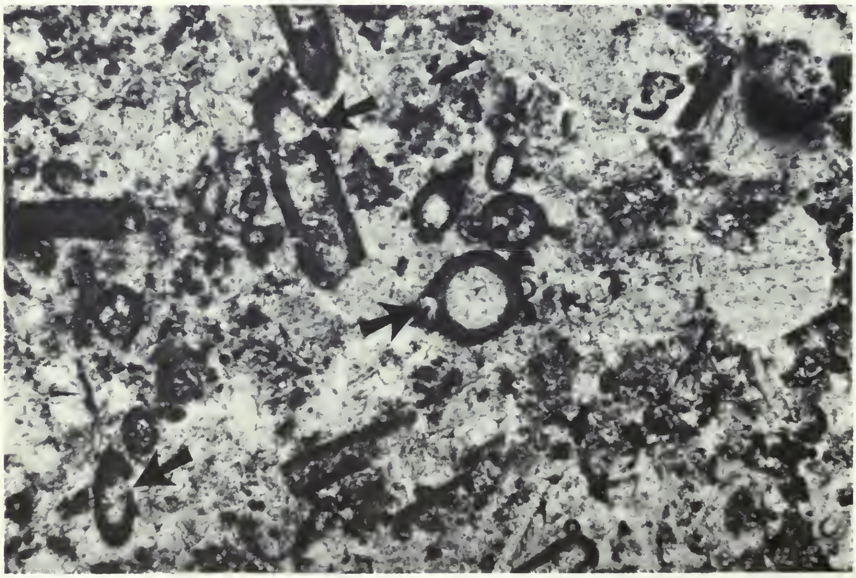

Fig. 2 *Uraloporella* showing speckled wall structure and partial recrystallization of walls (arrowed). Note cloudy matrix. *Uraloporella* Bed, Pwll-du Quarry (National Grid ref. SO 2495 1170; Wright 1981*a*: 348). British Museum (Natural History) Dept Palaeontology, reg. no. V.60808a. Field of view is 4 mm wide.

structure and appears to have been prone to recrystallization, often having diffuse edges. No branched tubes have been seen. Poorly preserved septa occur but are not common. The sparry calcite matrix surrounding the fragments is cloudy (Figs 1, 2); this is partly owing to the presence of crinoid fragments with syntaxial overgrowths but appears to be mainly because of the patchy recrystallization of the tubes. Details of the neomorphic fabrics are difficult to elucidate.

The features described above are consistent with the emended diagnosis of *Uraloporella variabilis* Korde (Riding & Jansa 1974 : 1412), although as Fig. 3 shows these Carboniferous forms are slightly larger than those described from the Middle Devonian of Germany (Faber & Riding 1979) and the Middle–Upper Devonian of Alberta (Riding & Jansa 1974). Recrystallization has probably destroyed many of the smaller forms. Comparisons between these Carboniferous forms and material from the Devonian of Alberta shown to me by Robert Riding (Cardiff) confirms the identification as *Uraloporella*. This microfossil was interpreted as a dasycladacean alga (Korde 1950) but has been reinterpreted as a possible foraminifer belonging to the Nodosinellidae (Riding & Jansa 1974 : 1422). Termier *et al.* (1977) have classified *Uraloporella* in the Moravamminida, an order of their class Ischyrospongia (Porifera).

This microfossil has been recorded from the Middle Carboniferous of the Urals (Korde 1950), the Cantabrian Mountains of Spain (Racz 1965) and arctic Canada (Mamet *et al.* 1979); the Givetian–Frasnian of Alberta (Riding & Jansa 1974) and Western Australia (Riding & Jansa 1976); the Givetian of the Eifel, West Germany (Faber & Riding 1979) and the Frasnian of the Holy Cross Mountains, Poland (Kaźmierczak & Goldring 1978). Thus *Uraloporella* has a range from Middle Devonian to Middle Carboniferous (Moscovian) or even to the Lower Permian (Sakmarien) (see Mamet *et al.* 1979).

The recognition of the Devonian representatives as *Uraloporella* has been challenged by Mamet & Roux (1975), who reclassified the Albertan (Devonian) specimens as a new form *Jansaella ridingi* Mamet & Roux. They rejected the Albertan forms as *Uraloporella* because, they claimed, the type material of *Uraloporella* does not have regularly-spaced septa. From my own examination of the Albertan forms, and the Lower Carboniferous forms described here, and from the descriptions of Riding & Jansa (1976) and Faber & Riding (1979), it is clear that all these specimens are of *Uraloporella* Korde 1950 (emend. Riding & Jansa, 1974). These microfossils show variable preservation of the septa, so that some forms show regular well-preserved septa (e.g. Riding & Jansa 1974 : pl. 1, fig. 2), while others show very poorly preserved septa as in the topotype material from the Ural Mountains (see Riding & Jansa 1974 : pl. 2). Mamet & Roux (1975) have called the better-preserved forms *Jansaella ridingi*. This problem clearly shows the need for the careful differentiation of diagenetic effects from primary, biogenic features, as the author has stressed elsewhere (Wright 1981*b*).

Stratigraphical and Environmental Distribution

As a result of their narrow definition of this microfossil Mamet & Roux (1977 : 247) state that *Uraloporella* is not known below the Middle Carboniferous. But using the emended diagnosis of Riding & Jansa (1974) the genus occurs in the Arundian (Viséan) limestones, and obviously in the Devonian. What is unusual about the range of this form in the Arundian limestones is that it only occurs at one horizon; it has not been found below in similar lithologies in the Llanelly Formation and is also absent in the overlying oolitic lithofacies of the Penllwyn Oolite Member. Since this form has a wide stratigraphical range its restricted distribution here is difficult to explain, but it is obviously a very useful marker locally.

One reason why this microfossil has not been previously recorded in Britain may be that since it is rather prone to recrystallization, losing its radial wall structure, it can easily be misinterpreted as a micritized brachiopod spine. Mr R. Barraclough (University of Leeds) has informed me that some of the problematical 'mud-mounds' in the Lower Carboniferous

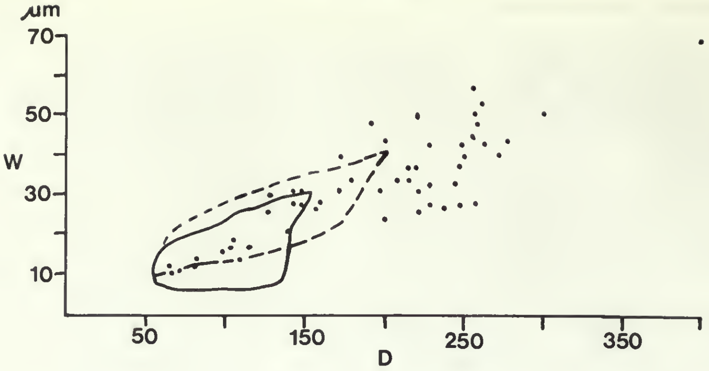

Fig. 3 Plot of the dimensions of *Uraloporella* from the *Uraloporella* Bed at various localities. W, wall thickness; D, external tube diameter (µm). The solid line marks the limit of distribution of the Middle Devonian forms from Germany (Faber & Riding 1979 : fig. 3), and the dashed line marks the limit of distribution of specimens from the Devonian of Alberta (Riding & Jansa 1974 : fig. 5).

of northern England contain large numbers of poorly preserved brachiopod spines (*Uraloporella*?) but are not found with brachiopod shells. Possibly some of these mud mounds contain *Uraloporella* bafflestones similar to those described by Mamet *et al.* (1979) from the Middle Moscovian of the Canadian Arctic archipelago.

Uraloporella is frequently found in back-reef and restricted lagoonal deposits (Riding & Jansa 1974, 1976; Kaźmierczak & Goldring 1978; Faber & Riding 1979). In the present Carboniferous occurrence *Uraloporella* is associated with fragments of brachiopods and crinoids suggesting fully marine conditions although there is some evidence locally of schizohaline conditions at this horizon (Wright 1981*c*). Restricted lagoonal deposits are represented in the Llanelly Formation below the *Uraloporella* Bed (Wright & Wright 1981) but do not contain *Uraloporella*. The conclusion of Faber & Riding (1979) that *Uraloporella* preferentially occurs in protected lagoonal environments seems suspect and this form should not be used as a facies indicator.

Acknowledgements

I thank Dr Robert Riding (University College, Cardiff) for reading an earlier draft of this work and for showing me some of the Albertan material. I also thank Dr Graham F. Elliott of the Department of Palaeontology, BM(NH) for constructively reading an earlier draft. Miss Paula Westall kindly typed the manuscript.

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Geology series
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The Ordovician Graptolites of Spitsbergen

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Synopsis

The Valhallfonna Formation, northern Ny Friesland, Spitsbergen, includes 56 species and subspecies of graptoloids, which occur in intimate association with rich trilobite faunas. The faunas range in age from early Arenig (Bendigonian) to probably earliest Llanvirn. The Arenig age faunas of the Olenidsletta Member include a number of samples of beautifully preserved, isolated material, from horizons which have never hitherto yielded such well-preserved specimens. These contribute to an understanding of general phylogenetic relationships in the early history of dichograptoids.

We introduce some revisions in the descriptive terminology and thecal notation system for dichograptoid graptoloids. The principles of classification of these graptoloids are discussed, and a system based on early rhabdosome development is preferred. It is established that the isograptid development type (with th1^2 dicalycal) is primitive for the Graptoloidea, and it is the rule for our Arenig species. The *artus* development type (formerly, and incorrectly, termed the *bifidus* type), with th1^1 dicalycal, is secondarily derived from the isograptid type. Two major development styles are recognized in graptoloids with dichograptid grade of organization: these characterize the families Dichograptidae and Phyllograptidae, both redefined here.

Three subfamilies are recognized in the Dichograptidae: Dichograptinae, Isograptinae and Sigmagraptinae nov., the last defined by a slender proximal end with a characteristic structure. In general we employ the well-established form-genera *(Didymograptus, Tetragraptus),* using subgenera to typify phylogenetic groupings within genera; one new such subgenus, *Didymograptus (Didymograptellus)* is proposed. The development and fine structure of the type species of *Phyllograptus, P. typus,* shows that it is not related to superficially similar phyllograptoids of the *angustifolius* group: for these the new dichograptid genus *Pseudophyllograptus* (type species *P. angustifolius* Hall) is proposed. *Phyllograptus* in the restricted sense is related to a group of extensiform 'didymograptids' which are placed in the new genus *Xiphograptus* (type species *D. formosus* Bulman). *Xiphograptus* and *Phyllograptus* together constitute the Phyllograptidae.

In addition to the foregoing, the following new taxa are proposed: *Laxograptus* gen. nov. (a sigmagraptine, type species *Zygograptus irregularis* Harris & Thomas); *Dichograptus maccoyi densus* subsp. nov.; *Tetragraptus contrarius* sp. nov.; *Tetragraptus phyllograptoides triumphans* subsp. nov.; *Didymograptus (Didymograptellus) multiplex* sp. nov.; *Pseudophyllograptus angustifolius chors* subsp. nov.; *Isograptus scandens* sp. nov. *Pseudotrigonograptus* exists in both triserial and quadriserial morphs; for the former the specific name *P. minor* Mu & Lee is employed, for the latter *P. ensiformis* (Hall).

Lectotypes are designated for the following species of J. Hall (1858, 1865): *Tetragraptus bryonoides, Didymograptus extensus, D. similis, D. patulus, Phyllograptus typus, P. ilicifolius, P. angustifolius* and *P. anna*; also for *Tetragraptus amii* and *T. reclinatus* Elles & Wood 1902, and for *Tetragraptus serra* (Brongniart 1828) the type specimens of which have been rediscovered.

The Spitsbergen graptolites are typical of the Pacific Province, and the Australian and New Zealand succession can be matched zone by zone in the Valhallfonna Formation. Stratigraphic distribution of the species shows that the Arenig Series divides naturally into three; Lower Arenig, *approximatus* faunas at base and extending upwards to the diverse later Bendigonian; Middle Arenig, an interval characterized by the first radiation of pendent didymograptids and true *Phyllograptus*; and Upper Arenig, the major radiation of the isograptids, with *Pseudotrigonograptus* and *Xiphograptus*. *Pseudophyllograptus* occurs in the Lower and Upper, but not the Middle Arenig in Spitsbergen. This tripartite division is probably generally applicable in the Pacific Province. Equivalents of what we here term Upper Arenig are attenuated or absent on platform sequences on what were separate continental blocks in the early

Ordovician; this is probably attributable to the effects of a major marine regression coinciding with Upper Arenig (= Valhallan Stage) deposition in Spitsbergen.

Introduction and acknowledgements

This paper describes the Ordovician graptolites from the Valhallfonna Formation (Arenig–?Llanvirn), Ny Friesland, northern Spitsbergen. The graptolite fauna in the Valhallfonna Formation is a varied one. Although much of the material is preserved as flattened rhabdosomes, a number of species are preserved in relief, and can be isolated from the rock by solution in acid. Very few graptolites of this age have been described from isolated material, and it is our belief that this new information contributes to an understanding of the phylogeny of the Graptoloidea as a whole. From a stratigraphical point of view the Valhallfonna graptolites are of special importance because they occur with possibly the richest trilobite faunas of any succession of early Ordovician age, which have been described in a series of papers by Fortey (1974, 1975*a,* 1980*a*). There is no other section on the North American Ordovician plate where such a rich Arenig graptolite assemblage can be directly linked with a succession of trilobite faunas. The Valhallfonna sequence is also a thick one, and there is every reason to suppose that the succession of graptolite faunas recorded in it is complete; bed-by-bed collecting has enabled refinements to be made to the zonal sequence of graptolite faunas.

The material which forms the basis of this paper was collected either by the Cambridge University Expedition of 1967, or by that run by the Norsk Polarinstitutt and the Paleontological Museum, Oslo in 1972. Specimens are stored in the Sedgwick Museum, Cambridge (SM), the Paleontological Museum, Oslo (PMO) and British Museum (Natural History). Many of the species names employed here have a long history, and in many cases we have examined type material to support our determinations. The following have assisted us in the search for specimens in their collections: Dr T. E. Bolton, Geological Survey of Canada, Ottawa; Dr J. N. Krumdieck, New York State Museum; Miss E. Lilljehall, Geological Collections, Lunds Universitet, Sweden; Dr R. B. Rickards, Sedgwick Museum, Cambridge; Dr A. W. A. Rushton, Institute of Geological Sciences, London; Dr D. L. Bruton, Palaeontological Museum, Oslo. The larger part of the contribution of R.A.C. was completed during the tenure of a Nuffield Travelling Fellowship and a Study Award supported by the Department of Scientific and Industrial Research, New Zealand, which are gratefully acknowledged. Most of the photography was undertaken by the Photographic Unit of the British Museum (Natural History).

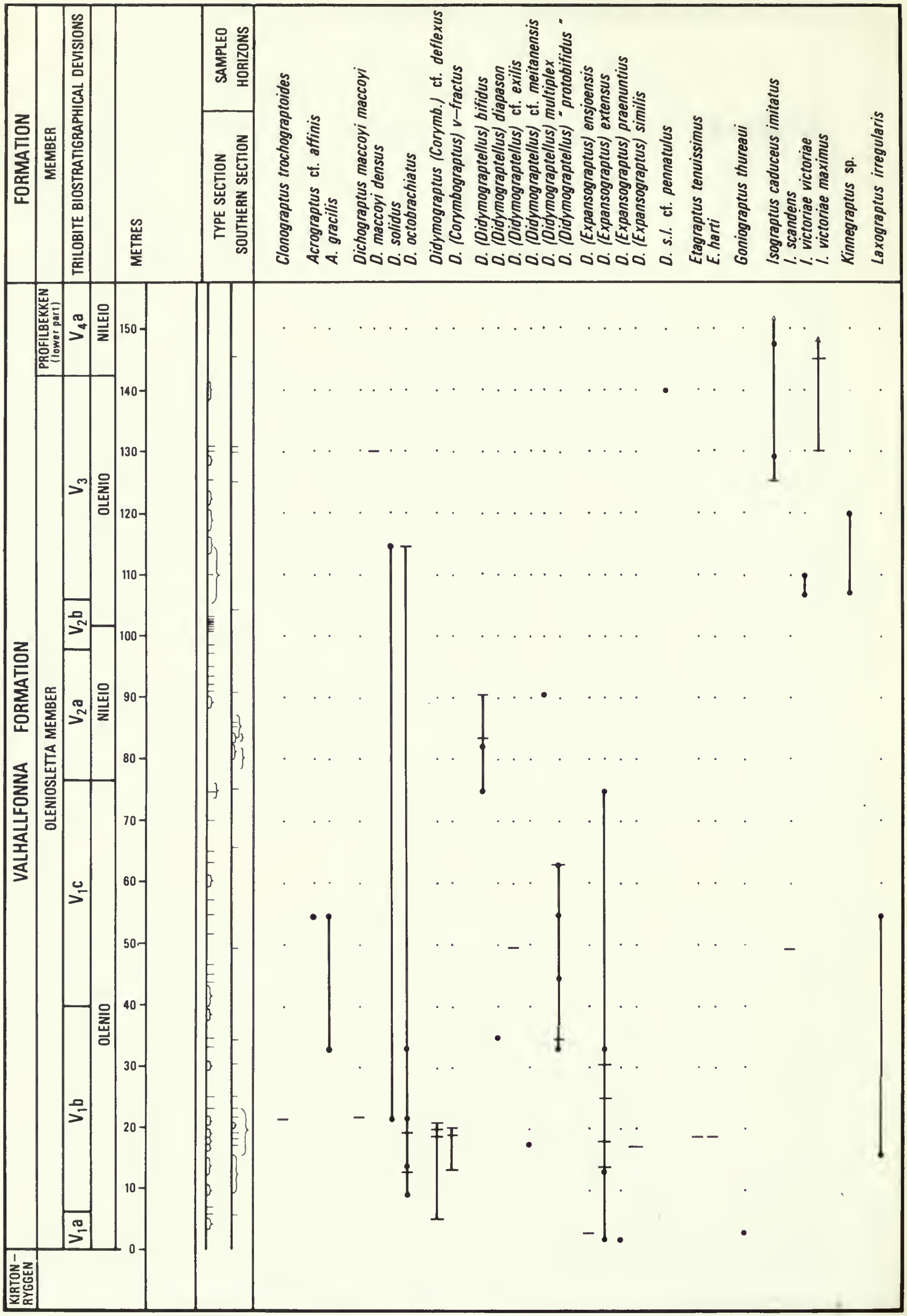
Stratigraphy

The regional geology, general stratigraphy and lithologies of the Valhallfonna Formation were described by Fortey & Bruton (1973) and Fortey (1975*b*). Specific comments on the age of the graptolite faunas have been given by Fortey (1971, 1976, 1980*a*) and Archer & Fortey (1974). Our more detailed work on the graptolites confirms in general the age determinations of the earlier work, although we now have a more refined biostratigraphy. The Valhallfonna Formation was deposited over a period extending from the early Arenig (Upper Bendigonian = higher part of the *T. fruticosus* Zone) to probably the earliest Llanvirn. The most prolific faunas are found in the lower unit, the Olenidsletta Member, which is generally developed in deeper water facies than the overlying Profilbekken Member. The Olenidsletta Member includes the Bendigonian faunas at its base and extends into the high Castlemainian. A more detailed account of the sequence of faunas is given below.

Occurrence of the graptolites

Graptolites occur in three main types of preservation in the Valhallfonna Formation:

1. As flattened impressions on dark limestones, lime-shales, or, rarely, fine silty shales without carbonate. This last is the ‘usual’ mode of preservation of graptoloids. Fine details of


FORMATION
MEMBER
TRILOBITE BIOSTRATIGRAPHICAL DEVISIONS
METRES
SAMPLED HORIZONS
TYPE SECTION
SOUTHERN SECTION
KIRTON-RYGGEN
VALHALLFONNA FORMATION
OLENIOSLETTA MEMBER
PROFILBEKKEN (lower part)
V1a
V1b
V1c
V2a
V2b
V3
V4a
OLENIO
NILEIO
OLENIO
NILEIO
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
Clonograptus trochograptoides
Acrograptus cf. affinis
A. gracilis
Dichograptus maccoyi maccoyi
D. maccoyi densus
D. solidus
D. octobrachiatus
Didymograptus (Corymb.) cf. deflexus
D. (Corymbograptus) v–fractus
D. (Didymograptellus) bifidus
D. (Didymograptellus) diapason
D. (Didymograptellus) cf. exilis
D. (Didymograptellus) cf. meitanensis
D. (Didymograptellus) multiplex
D. (Didymograptellus) " protobifidus "
D. (Expansograptus) ensjoensis
D. (Expansograptus) extensus
D. (Expansograptus) praenuntius
D. (Expansograptus) similis
D. s.l. cf. pennatulus
Etagraptus tenuissimus
E. harti
Goniograptus thureaui
Isograptus caduceus imitatus
I. scandens
I. victoriae victoriae
I. victoriae maximus
Kinnegraptus sp.
Laxograptus irregularis

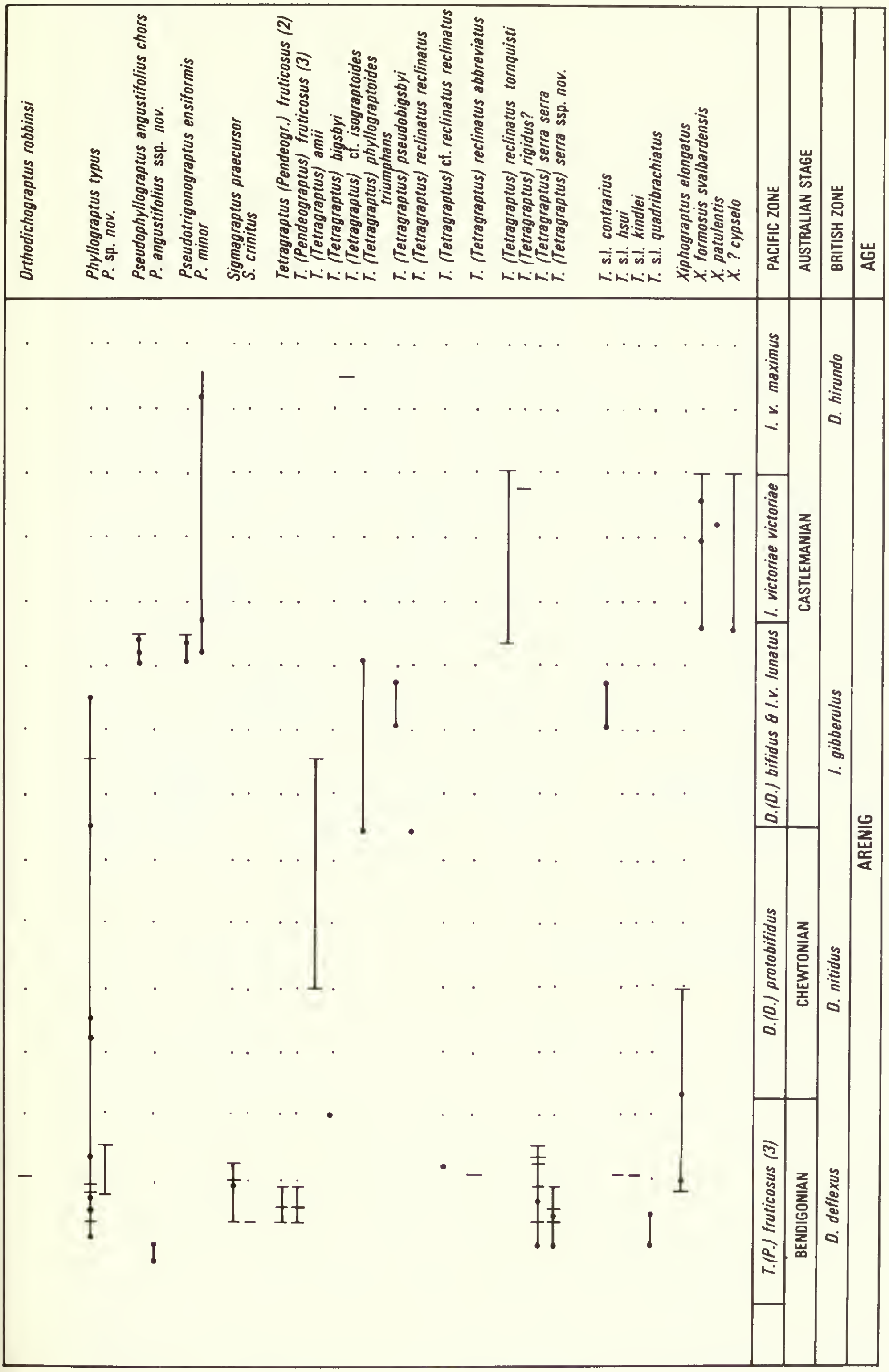


Fig. 1 Range chart of species in Spitsbergen succession.

thecal structure are obscured. Generally the periderm is black and carbonized and hence hard to photograph, except in the rare cases where they have acquired a silvery sheen. We have to rely on line drawings to illustrate this kind of material.

2. In relief in limestone, but without the capacity for isolation. The periderm in these cases is reduced to a carbonaceous film, whch breaks up into unidentifiable black specks on solution in acid. We have used serially ground sections to study fine anatomy of this kind of material, which gives good results. Such preservation is commonest in rather pure limestones, such as those at the top of V_2 in the Olenidsletta Member, and it is possible to infer a good deal about three-dimensional structure even without serial sections (e.g. *Pseudotrigonograptus ensiformis,* p. 249).

3. In relief in limestone, and with periderm well enough preserved for isolation. The commonest lithology for this kind of preservation is an impure, dark limestone with a high silt (and often silica) content. The material described by Fortey (1971) and Archer & Fortey (1974) was from beds of this kind. We now have a spread of such horizons through most of the Olenidsletta Member. In rare cases the material is flattened, although it can still be isolated. Proximal ends are often partially translucent, and growth stages are common enough to reconstruct astogeny. Curiously, most of the productive horizons are almost monospecific. The most striking case of this is perhaps the horizon that yielded the triserial *Pseudotrigonograptus minor* described by Fortey (1971). This species is generally rare in the upper 40 m of the Olenidsletta Member. The bed in which the material which it is possible to isolate occurs is crowded with rhabdosomes at all stages of growth. One must presume that the species lived together in large clots or drifting swarms which, rarely, were overcome *in toto* (plankton bloom?), and, losing buoyancy, ultimately came to rest as a thick layer on the sediment surface. A few specimens of *Xiphograptus formosus svalbardensis* were entrapped at the same time. Another horizon, only a few metres above that with *Pseudotrigonograptus,* is crowded with the rhabdosomes of *X. formosus svalbardensis,* but with *Pseudotrigonograptus* extremely rare, and tetragraptids likewise. There is nothing to suggest protracted non-deposition at such horizons, indeed, it would be difficult to explain the preservation in relief if the specimens were not enclosed by sediment relatively quickly. Some graptoloids may have been gregarious, like some of the open ocean siphonophores today, and monospecific horizons may be the record of foundered swarms of gregarious species. The restricted diversity of these horizons means that in such cases it is relatively easy to associate growth stages with the appropriate mature rhabdosome; the relief specimens command a large share of the present systematic treatment. Many of our species, however, have not been recovered from such horizons, and are known only from flattened examples.

Sequence and correlation of graptolite faunas

The general sequence of graptolite faunas in the Valhallfonna Formation was given by Fortey (1976, 1980*b*). We have now been able to plot the detailed stratigraphic ranges of the species (Fig. 1), both from the southern and northern sections of the Olenidsletta Member. There is no significant difference in the sequence of faunas between the sections, although some of the best fossiliferous horizons, such as those described in the previous paragraph, are not traceable from one section to the other. For example, one important bed at 50 m from the base of the Olenidsletta Member has yielded a rich fauna in the southern section, including *Isograptus scandens* sp. nov., but has not been found in the northern section.

There is no evidence in the Olenidsletta Member of the earliest Arenig faunas of the *Tetragraptus approximatus* Zone. Strata equivalent to this zone are probably present in the upper part of the underlying Kirtonryggen Formation, which has a fauna very similar to that of the Catoche Formation, western Newfoundland, of probable *T. approximatus* Zone age. Stratigraphic plots of the ranges of the graptoloid species from the Olenidsletta Member show that there is a great deal of overlap between ranges, and hardly any sharp breaks in the sequence, which is no doubt a reflection of the thickness of the succession and a lack of major hiatuses in deposition. Nonetheless it is possible to recognize a succession of zonal assemblages exactly comparable to those recognized in other successions of the Pacific province, such as in

Texas, Australia and New Zealand. In our account we generally refer to the stage names used in the sequence of Victoria, Australia (Thomas 1960), because they include the most refined divisions, but which also have their equivalents in the scheme of Berry (1960), widely used in North America. Correlation with the standard sequence of Great Britain and that of Scandinavia is inferred from more slender evidence (Fig. 2).

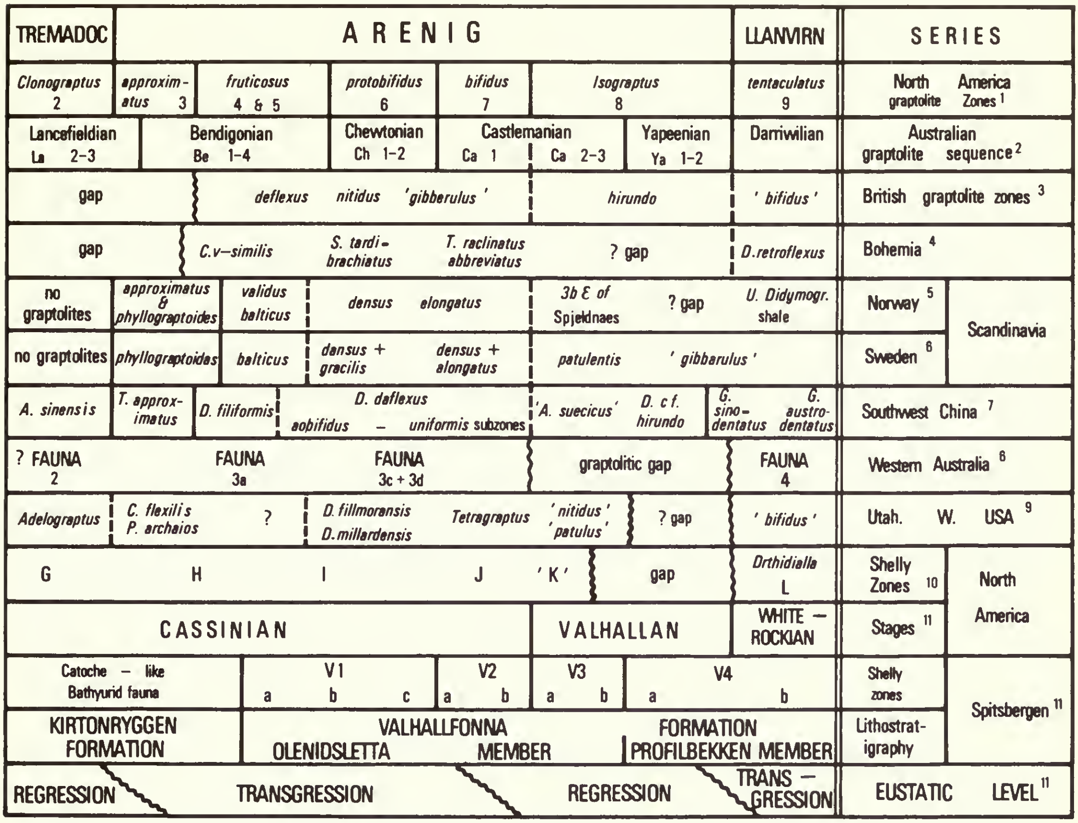

TREMADOC
A R E N I G
LLANVIRN
S E R I E S
Clonograptus 2
approximatus 3
fruticosus 4 & 5
protobifidus 6
bifidus 7
Isograptus 8
tentaculatus 9
North America graptolite Zones 1
Lancefieldian La 2-3
Bendigonian Be 1-4
Chewtonian Ch 1-2
Castlemanian Ca 1
Ca 2-3
Yapeenian Ya 1-2
Darriwilian
Australian graptolite sequence 2
gap
deflexus
nitidus
'gibberulus'
hirundo
' bifidus '
British graptolite zones 3
gap
C.v–similis
S. tardi-brachiatus
T. raclinatus abbreviatus
? gap
D.retroflexus
Bohemia 4
no graptolites
approximatus & phyllograptoides
validus balticus
densus
elongatus
3b Ɛ of Spjeldnaes
? gap
U. Didymogr. shale
Norway 5
no graptolites
phyllograptoides
balticus
densus + gracilis
densus + elongatus
patulentis
' gibbarulus '
Sweden 6
Scandinavia
A. sinensis
T. approximatus
D. filiformis
D. daflexus
eobifidus – uniformis subzones
'A. suecicus'
D. cf. hirundo
G. sino-dentatus
G. austro-dentatus
Southwest China 7
? FAUNA 2
FAUNA 3a
FAUNA 3c + 3d
graptolitic gap
FAUNA 4
Western Australia 8
Adelograptus
C. flexilis
P. archaios
?
D. fillmorensis
D. millardensis
Tetragraptus
'nitidus'
'patulus'
? gap
' bifidus '
Utah. W. USA 9
G
H
I
J
'K'
gap
Orthidiella L
Shelly Zones 10
North America
CASSINIAN
VALHALLAN
WHITE – ROCKIAN
Stages 11
Catoche – like Bathyurid fauna
V1 a b c
V2 a b
V3 a b
V4 a b
Shelly zones
KIRTONRYGGEN FORMATION
VALHALLFONNA FORMATION
OLENIDSLETTA MEMBER
PROFILBEKKEN MEMBER
Lithostratigraphy
Spitsbergen 11
REGRESSION
TRANSGRESSION
REGRESSION
TRANS – GRESSION
EUSTATIC LEVEL 11

Fig. 2 Correlation of early Ordovician sequences, late Tremadoc to early Llanvirn. Note the gap in the Late Arenig record of many areas, especially in cratonic regions. References: 1, Berry (1960); 2, Thomas (1960); 3, Elles & Wood (1901–18), Jackson (1962); 4, Bouček (1973); 5, Monsen (1937); 6, Tjernvik (1960); 7, Mu *et al.* (1979); 8, Legg (1976); 9, Braithwaite (1976); 10, Ross (1951); 11, Fortey (1980*b*).

1. Late Bendigonian (late *T. fruticosus* Zone). The lower part of the Olenidsletta Member, certainly embracing the lower 20 m, has a rich fauna of later Bendigonian age (and equivalent to Berry's Zone 5, *T. fruticosus* three-branched). The earliest graptolite-bearing beds of the Olenidsletta Member contain a stout extensiform species which we have identified with *Didymograptus (Expansograptus) praenuntius,* which is most abundant in the *Phyllograptus densus* Zone in Sweden (Tjernvik 1960). The fauna in the succeeding black, flaggy limestone-shale is flattened, and is a typical later Bendigonian (Be 3–4) assemblage, including the three-branched and two-branched forms of *Tetragraptus fruticosus, T. serra* (large robust forms here), *T. quadribrachiatus, Didymograptus (Expansograptus) extensus, D. (E.) similis, Goniograptus thureaui, Sigmagraptus crinitus, S. praecursor, Etagraptus tenuissimus, Dichograptus octobrachiatus* (abundant), several deflexed didymograptids, *Pseudophyllograptus angustifolius* subsp. nov. (see p. 247), *Clonograptus trochograptoides* and *Orthodichograptus robbinsi.* The earliest pendent didymograptid occurs in this interval, *D.* cf. *meitanensis.*

This is a fauna exactly comparable with that from the type Bendigonian of Australia; indeed, *Sigmagraptus crinitus, Clonograptus trochograptoides* and *Orthodichograptus* have not previously been recorded from outside Australia. Yet the presence of deflexed didymograptids of *D. v-fractus* and *deflexus* type is more like the British early Arenig, and Jackson (1962) records these species as typical of the earliest *(D. deflexus* Zone*)* strata in the Lake District.

2. Chewtonian–earliest Castlemainian (*D. 'protobifidus' – D. bifidus* Zones). This interval intergrades perfectly with the Bendigonian below, and accounts for the middle part of the Olenidsletta Member, from 30 m to 105 m from base. It is convenient to discuss the *D. 'protobifidus'* and *D. bifidus* Zones together because they also intergrade perfectly – the eponymous species change between their typical morphologies in an entirely gradualistic fashion (see p. 224). As a whole the interval is characterized by an abundance of 'tuning fork' didymograptids and true *Phyllograptus*. The latter is distinguished in this paper from *Pseudophyllograptus* – a genus found both below and above (*P. angustifolius* s. str.), but not, in Spitsbergen at least, in this middle part of the Arenig. A number of the Bendigonian species carry on through varying parts of this interval – *Tetragraptus serra* and *Didymograptus (Expansograptus) extensus* are examples – but others (e.g. *Dichograptus octobrachiatus*) are much rarer than in lower strata. In the earlier part of the interval (*D. 'protobifidus'* Zone) the following species are characteristic: *Didymograptus (Didymograptellus) 'protobifidus', D. (D.) diapason, D. (D.)* cf. *exilis, Phyllograptus typus, Tetragraptus amii, Laxograptus irregularis, Dichograptus octobrachiatus, Xiphograptus elongatus, Acrograptus gracilis* and the peculiar early *Isograptus, I. scandens* sp. nov. (p. 257).

The *D. bifidus* interval is typically developed between 75 and 90 m from base of the Olenidsletta Member, with gradation downwards into the *'protobifidus'* Zone. The same interval includes a short-lived shallowing event in the deposition of the Olenidsletta Member, which produced a drastic change in the trilobite faunas compared with those above and below, including the disappearance of the varied olenid trilobites with which abundant graptolites are normally associated in Spitsbergen. This change in facies may account for a general scarcity of graptolites through this interval, but a few horizons are productive. Typical species include: *Didymograptus (Didymograptellus) bifidus, Phyllograptus typus, Tetragraptus phyllograptoides triumphans* subsp. nov. (p. 200) and *T. reclinatus reclinatus.* In the upper part of the interval there is a horizon with the particular graptolites *Tetragraptus contrarius* sp. nov. (p. 213) and *Didymograptus (Didymograptellus) multiplex* sp. nov. (p. 229) together with *T. pseudobigsbyi.* The upper few metres of the interval contain little except *Pseudophyllograptus angustifolius chors* subsp. nov. (p. 244), *Tetragraptus phyllograptoides triumphans* and *Pseudotrigonograptus* in rather coarsely crystalline limestones. These beds are transitional in lithology and trilobite faunas between the nileid facies below and the olenid facies above, and the faunal changes in the benthic elements have been described in detail (Fortey 1975*b*: fig. 4). *Pseudotrigonograptus ensiformis,* with four thecal series, slightly precedes a species with three thecal series (*P. minor,* described by Fortey, 1971, as *'Tristichograptus ensiformis'*).

It is a curious fact that the *D. bifidus* Zone (*sensu* Berry, 1960) is not recognized in certain of the Pacific Province sections (e.g. New Zealand, Cooper 1979; Idaho, Carter & Churkin 1977). As noted above, its presence in Spitsbergen is associated with a short-lived shallowing event in the otherwise olenid trilobite facies of the Olenidsletta Member. In the more oceanic facies, such as those represented in the Idaho and New Zealand sections, its place appears to be taken by a short interval in which *Isograptus victoriae lunatus* is a common species. No *Isograptus* species occurs within the *D. bifidus* Zone in Spitsbergen: this may be a case of facies control, because *Isograptus* species are known both above and below in the olenid facies. The *bifidus* interval in Spitsbergen is overlain by large populations of *I. victoriae victoriae,* and is thus equivalent to the lower part of the Castlemainian Stage, Ca 1, of Australia, and lower *I. v. lunatus* Zone of New Zealand.

3. Later Castlemainian *(Isograptus victoriae victoriae – I. v. maximus).* This interval, equivalent to part of Berry's (1960) *Isograptus* (8) Zone, comprises the upper 40 m of the Olenidsletta Member. Previous studies on the Spitsbergen graptolites (Fortey 1971, 1976;

Archer & Fortey 1974) have been concerned mostly with species from this part of the section. As a whole it marks a return to the deep, oxygen-poor conditions to which the olenid trilobites were adapted, such as was the case for the Bendigonian–Chewtonian interval of the lower Olenidsletta Member. The fauna of the upper part of the Olenidsletta Member includes the following species: *Xiphograptus formosus svalbardensis*, *X. patulentis*, *X.* ?*cypselo*, *Tetragraptus reclinatus toernquisti*, *Didymograptus (Expansograptus)* cf. *pennatulus*, *Kinnegraptus* sp., *Isograptus victoriae victoriae*, *I. victoriae* cf. *maximus* and *Dichograptus maccoyi densus* subsp. nov. (p. 186). The age determination of the fauna is well founded; there are none of the elements of typical Yapeenian assemblages such as *Isograptus divergens* or the *Oncograptus–Cardiograptus* group. Some of the *I. victoriae* specimens appear to bear incipiently manubriate proximal ends, but there is no evidence of true *Pseudisograptus* in the Olenidsletta Member.

Berry's (1960) Zone 8 of *Isograptus* was a rather coarse division, and the upper Olenidsletta fauna represents only the early half of that zone. As far as Cooper's (1973) zonation in New Zealand is concerned the fauna fits into the *upper* half of his *Isograptus victoriae lunatus* Zone, the earlier part of which is equivalent to our *D. bifidus* interval. *Pseudotrigonograptus* occurs with a *D. hirundo* Zone fauna in Norway (see p. 250), and the same genus (both triserial and quadriserial) has been recovered by one of us (R.A.F.) from a high Arenig, probably *D. hirundo* Zone, fauna in south Wales, while Jackson (1962) records *P. ensiformis* from the *D. hirundo* Zone in the Lake District (but not from below that zone). If the first appearance of this highly distinctive graptoloid, one of the few distinctive species at this horizon, can be taken as a simultaneous event, then the base of the *D. hirundo* Zone should lie just above the first appearance of *Isograptus victoriae victoriae*. The first appearance of true biserial graptoloids occurs in the same zone in some sections. In south-west China (Mu *et al.* 1979) the first *Glyptograptus*, *G. sinodentatus*, occurs immediately below *Pseudotrigonograptus* (which is there associated as usual with *G. austrodentatus*) and in that area it is the *Isograptus* species which are apparently absent.

4. Late Castlemainian–Yapeenian. The passage upwards into the Profilbekken Member marks a general shallowing, and the graptolites become progressively rarer. The lowest part of the Member has yielded good specimens of *Isograptus victoriae maximus* and *I. caduceus imitatus* (see Fortey 1976), together with *Pseudotrigonograptus minor*, so that presumably the base of the Member is still within the top of the Castlemainian and the Member itself passes upwards into the Yapeenian. The Arenig–Llanvirn boundary lies somewhere within the considerable thickness of the Profilbekken Member. The occurrence of *Paracardiograptus* ? at 65 m from the base of the Member may indicate a horizon as young as the *Paraglossograptus tentaculatus* Zone (Llanvirn); from the same horizon come fragmentary robust stipes like those of a reclined tetragraptid species such as is found in the Ningkuo Shale of China and Yapeenian of Australasia. Green shales at the very top of the Profilbekken Member yield many specimens of *Tetragraptus* cf. *isograptoides*, also known from the Ningkuo Shale. Trilobite evidence (Fortey 1980*a*: 13–14), itself rather indirect, suggests that the best placing for the Arenig–Llanvirn boundary would be between the two successive shelly faunas of the Profilbekken Member (V_4a and V_4b). The graptolite material, so far as it goes, is not inconsistent with such a placement.

General history of Arenig graptolite faunas, Pacific province

A few general comments on the history of Arenig graptolite faunas in the Pacific Province are given here. As will become apparent from the systematic section below, many of the problems in the dichograptoids are nomenclatorial ones, but it is still possible to recognize certain broad features (Fig. 3) of the succession of Arenig graptolites throughout the Pacific Province if such nomenclatural *minutiae* are disregarded. We stress that these generalizations apply to the Pacific Province only – the broad belt to either side of the Ordovician palaeoequator, extending from North America, Greenland and Spitsbergen through the Tamir Peninsula, north-east

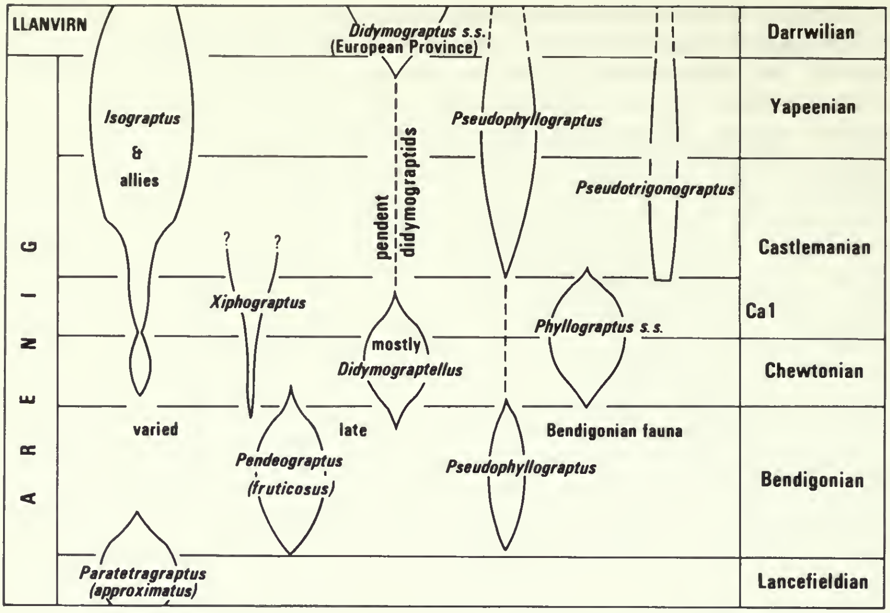

LLANVIRN
A R E N I G
Darrwilian
Yapeenian
Castlemanian
Ca1
Chewtonian
Bendigonian
Lancefieldian
Didymograptus s.s. (European Province)
Isograptus & allies
Pseudophyllograptus
pendent didymograptids
Pseudotrigonograptus
? ?
Xiphograptus
Phyllograptus s.s.
mostly Didymograptellus
varied
late
Bendigonian fauna
Pendeograptus (fruticosus)
Pseudophyllograptus
Paratetragraptus (approximatus)

Fig. 3 Sequence of main dichograptoid groups in the Pacific Province. Although based mainly on dominance (relative abundance) it also reflects diversity in a general way.

Siberia, south-west China, to Australia and New Zealand. There is evidence that the sequence of events may have been different in areas – such as southern and central Europe – which were at higher latitudes in the early Ordovician.

1. The *Tetragraptus (Paratetragraptus)* radiation

The widespread occurrence of the H-shaped rhabdosomes of *Tetragraptus (Paratetragraptus) approximatus* and allied forms has been recognized for a long time (e.g. Skevington 1963). Although several species are involved, the abundance of these forms is stratigraphically limited to the earliest Arenig, although it has to be added that there is no proof of equivalent strata in the type Arenig of Wales. It seems reasonable to suppose that *Tetragraptus (Paratetragraptus)* is a monophyletic group. The Spitsbergen Arenig graptolitic succession begins too late to record this early radiation.

2. Phyllograptid history

In this paper we report the discovery that the phyllograptid grade of rhabdosome organization was reached by (at least) two different pathways. True *Phyllograptus,* based on the type species *P. typus* (Hall), has a fundamental structure quite different from the phyllograptids of '*angustifolius*' type described by Bulman (1963*a*). The latter (*Pseudophyllograptus* n. gen.) is in essence a scandent *Tetragraptus,* whereas the true *Phyllograptus* has a complex internal structure which perhaps could not have been derived from a normal dichograptoid at all. From a stratigraphical view the important point is that true *Phyllograptus* spp. are confined to an interval within the Middle Arenig in Spitsbergen, and, so far as we can judge from descriptions based on flattened material, elsewhere in the Pacific Province. We have found no convincing example of true *Phyllograptus* from the Atlantic Province. *Pseudophyllograptus,* usually recorded as *P. angustifolius,* occurs both below and above the *Phyllograptus* interval (which corresponds to the *D. protobifidus–bifidus* Zones), and it is possible that rhabdosomes of this organizational type were derived from *Tetragraptus* on two occasions. In this connection it is of interest that we have discovered a *Tetragraptus* of *phyllograptoides* type below our upper *Pseudophyllograptus,* and considerably younger than *T. phyllograptoides* from Scandinavia, which underlies the earlier *Pseudophyllograptus* burst. Several species of true *Phyllograptus* have been described by Mu *et al.* (1979), and again their stratigraphical distribution is consistent with what happens in Spitsbergen.

3. Pendent didymograptids

These somewhat intractable graptolites have generated a disproportionate amount of attention in the literature, because of an earlier belief that their main diversification occurred the world over in the early Llanvirn. This is not so. It has become apparent that there were two such events: one in the earlier Arenig, and again near the Arenig–Llanvirn boundary. In the Pacific Province, these episodes with pendents are separated by a stratigraphic gap, in which no pendent graptolites at all have been discovered: this corresponds to the interval, Castlemainian (Ca 2–3) and Yapeenian, well demonstrated by the upper part of the Olenidsletta Member in Spitsbergen. This disappearance of pendent forms is apparently sudden in Spitsbergen, and there seems no preservational cause to explain it. Part of the reason for the miscorrelation of the Arenig and Llanvirn pendent-bearing intervals was a scarcity of single sections in the Pacific Province spanning *both* radiations; two such have now been described, from Utah (Braithwaite 1976) and south-west China (Mu *et al.* 1979). In the latter the variation of rhabdosome form in the Arenig pendent didymograptids matches that usually associated only with the Llanvirn interval – broad, *D. murchisoni*-like, species are present, for example. We also have a few of these forms in Spitsbergen. Our discovery of isograptid development in one of the Arenig forms, and its inferred presence in others, contrasts with the *artus* type development of described Llanvirn species.

The combination of Arenig pendent didymograptids with *Phyllograptus, s.s.*, makes the Chewtonian – early Castlemainian interval a highly characteristic one. It forms the 'filling' between highly diverse later Bendigonian faunas below, and the main *Isograptus* radiation above. It would provide a natural way of discriminating a Middle Arenig from Lower and Upper Arenig intervals.

4. *Pseudotrigonograptus*

This distinctive genus has species with either three or four series of thecae. It is assuredly monophyletic, and so we do not have the kind of problems that have been encountered with *Pseudophyllograptus,* where the same grade of rhabdosome organization can be acquired in two or more lineages. As far as we can tell from the literature its first appearance is with or immediately before that of *Isograptus victoriae victoriae,* in sections containing both forms, and since the place of the latter within the evolving *Isograptus* plexus is now well known it is reasonable to conclude that *Pseudotrigonograptus* appears at about the same time in all sections. It is often found with *Didymograptus hirundo* (see p. 165), and it may be a reliable guide fossil for the correlation of that zone. It also always postdates the abundant record of *Phyllograptus, sensu stricto.*

5. *Isograptus*

The evolutionary history of species of *Isograptus* from Australasia was documented in detail by Cooper (1973), and it is encouraging for their use in correlation that the sequence of species in Spitsbergen is consistent with their occurrence in the southen hemisphere. The only modification to Cooper's account is the discovery of an early species (*I. scandens* sp. nov.) which anticipates within a single population some of the changes which were later undergone by the isograptids as a whole. Some individuals of *I. scandens* have become effectively scandent. Nonetheless, it remains true that the isograptids remain limited in abundance and variety until the mid-Castlemainian, when they commonly dominate assemblages on certain bedding planes. This expansion in numbers is coeval with the appearance of *Pseudotrigonograptus* and the disappearance of pendent forms commented on above. One might speculate that the isograptids, which are morphologically 'reversed tuning forks', somehow filled the ecological role vacated by the preceding *Didymograptus (Didymograptellus)* species.

6. *Xiphograptus*

One of the more surprising aspects of the isolated graptolites from the Spitsbergen Arenig was the discovery that there is a group of extensiform 'didymograptids' which are in fact more closely related to *Phyllograptus, sensu stricto,* than to other extensiforms of the subgenus *Didymograptus (Expansograptus)*; these are placed in our new genus *Xiphograptus* (p. 289). The new genus is present as a relatively minor element in early Arenig extensiform faunas, the familiar, widely-recorded species of Hall (*extensus, patulus, similis,* etc.) all being dichograptids of normal *(Expansograptus)* developmental type. But at least as far as the faunas from Spitsbergen are concerned, *Xiphograptus* spp. are the numerically dominant extensiforms in the mid-Castlemainian. Whether this is more general in the Pacific Province is not known, because very well preserved material is needed to discriminate *Xiphograptus* from other extensiforms, but it is suggestive that identical or closely related species are an important element in the latest Arenig faunas of Utah as well (Braithwaite 1976). Spitsbergen and Utah are some 5000 miles apart today, and probably a similar distance apart in the Ordovician; with this known spread, there seems to be no reason in principle why *Xiphograptus* should not have traversed the entire Ordovician equatorial great circle, like many of the other Pacific Province forms.

Summary

The Arenig Series of the Pacific Province is divided into three broad stratigraphical divisions on graptolite faunas:

1. Lower Arenig. *T. approximatus* Zone at base, extending upwards to the diverse, Late Bendigonian faunas of the *T. fruticosus* Zone.
2. Middle Arenig (Chewtonian and Ca 1). Arenig radiation of pendent didymograptids probably referable to *Didymograptus (Didymograptellus),* accompanied by true *Phyllograptus* of *typus* type, and allied species. An abundance of very slender sigmagraptines *(Sigmagraptus, Laxograptus, Acrograptus gracilis)* also appears to be characteristic.
3. Upper Arenig (Ca 2–3, Ya). Pendent didymograptids apparently absent; appearance of *Pseudotrigonograptus* and reappearance of *Pseudophyllograptus*; main isograptid radiation, and probably also that of *Xiphograptus.* Appearance of dipleural scandent graptolites.

The most fundamental division is between the Middle and Upper Arenig as defined here; many of the genera which were to dominate mid-Ordovician faunas probably have their roots in late Arenig species. The Arenig–Llanvirn boundary is not related to so profound a change in the graptolite faunas as that between the Middle and Upper Arenig as defined here: a renewed burst of pendent didymograptids is typical especially in the European Province, but the diplograptid, isograptid and glossograptid history in the Llanvirn is a continuation of that in the Upper Arenig.

Relation to trilobite faunas

Fortey (1980*a*) summarized the succession of the trilobite faunas through the Valhallfonna Formation. More than 100 species of trilobites have now been described from this formation, and the coexistence of such rich faunas, possibly the richest of this age anywhere, with varied graptolitic faunas is one of the reasons for the exceptional importance of the Spitsbergen Ordovician sequence. Fortey divided the Valhallfonna Formation into four major divisions (V_1 to V_4) from bottom to top, the boundaries between which marked changes in biofacies associated with particular suites of trilobite genera (Fortey 1975*b*). Within any one of these divisions, biostratigraphically significant assemblage zones in the same facies were designated by suffixes (V_1a, V_1b . . . etc.). The change from V_3 to V_4 at the boundary between the Olenidsletta and Profilbekken Members marks the beginning of the progressively shallowing sequence that closes Ordovician sedimentation in this area. These trilobite faunas can now be accurately calibrated against the graptolite ranges (Fig. 1, p. 160). In general the trilobites permit a somewhat finer division of the Valhallfonna Formation. On the other hand, so many of the trilobites, particularly the olenids, are not known elsewhere that the correlation potential of the benthic trilobite assemblages is at the moment limited. However, this does not apply to certain pelagic trilobites, such as *Carolinites* and *Opipeuter,* species of which are very widespread. These pelagic trilobites spread into areas without graptolites, and thus permit correlation between shelly faunal zones, such as those of Ross (1951) and Hintze (1953), and the graptolitic sequence in which they occur in Spitsbergen. This correlation has been described in some detail by Fortey (1976) and need not be repeated here, but the conclusions are summarized in Fig. 2 (p. 163).

Valhallan Stage and the late Arenig regression

One of the consequences of the correlation of the relatively deep-water Spitsbergen succession (up to V_4b) with platform sequences described from many sites in North America (Fortey 1980*b*) is the recognition of what appears to be a shelly faunal gap in these sequences below the earliest recognized Whiterock faunas (represented by V_4b in Spitsbergen) and above the highest recognized Canadian strata (V_2b in Spitsbergen). This was termed the Valhallan Stage (Fortey 1980*a*) and includes the succession of shelly faunas V_3a–b, V_4a.

In graptolitic terms the Valhallan can now be shown to be equivalent to the Ca 2–3 interval plus all or part of the Yapeenian, that is, with the important Upper Arenig interval described above (and probably equivalent to the British zone of *Didymograptus hirundo*). Fortey (1980*b*) indicated that the reason why the Valhallan shelly fossils are missing over much of platform North America was a regression below the Arenig–Llanvirn boundary, and suggested that this might prove to be so widespread as to imply a eustatic cause. If this were so its effects should be seen on what were separate plates in the Ordovician. We would predict that in epicratonic graptolitic sequences, where the regression would also produce seaward displacement of epieric facies, the characteristic *Isograptus victoriae victoriae – maximodivergens* fauna would be missing; true oceanic facies would, of course, be little affected. The following evidence suggests that the eustatic explanation may be the correct one.

1. In Australia Legg (1978) has described the stratigraphy of the Canning Basin, a peripheral cratonic succession with a mixed trilobite–graptolite fauna. His Fauna 3 contains a number of graptolites in common with the Spitsbergen succession, including typical representatives of the late Bendigonian and, above, pendent didymograptids and what is probably true *Phyllograptus,* indicating the presence of the '*protobifidus*'–*bifidus* interval. The succeeding Fauna 4 contains a wealth of biserial graptoloids, and other species which indicate a correlation with the Darriwilian. Thus there is a 'gap' in the succession of zones corresponding to the regression, and members of the typical *Isograptus* radiation are absent. Lithologies in the upper part of Fauna 3 tend to be limestones or sandstones, where Fauna 4 is accompanied by shale deposition.
2. In south-west China, according to the account of Mu *et al.* (1979), there is a richly fossiliferous equivalent of the *bifidus*–'*protobifidus*' interval, with what is without doubt true *Phyllograptus,* many pendent species, and a peculiar local radiation of deflexed forms. The pendent-bearing interval is followed by a zone of '*Azygograptus suecicus*' with variable populations of *Azygograptus* and *Phyllograptus,* some of the latter of which are almost certainly true *Phyllograptus* and not *Pseudophyllograptus*. The following zone of *D.* cf. *hirundo* is very impoverished in species, and those that are present are mostly curious, endemic many-branched species of *Schizograptus* and *Mimograptus*. The zone that follows *(Glyptograptus sinodentatus)* marks the appearance of *Pseudotrigonograptus* in these Chinese sections, with the first biserial graptoloid, and this is followed by strata of undoubtedly Llanvirn age with the second flowering of pendent didymograptids, accompanied by a diverse selection of biserial forms. Thus there is an interval through which pendent species are absent, and there is no evidence at all of the isograptids so typical of oceanic sequences in the late Arenig. The regressive phase is probably accommodated in the zones of *D.* cf. *hirundo* and *G. sinodentatus,* and possibly that of '*Azygograptus suecicus*' as well. In contrast to the Canning

Basin there are strata representing the interval, but these have a peculiar and endemic fauna, which we would regard as probably adapted to the inner shelf conditions of the shallower phase. True oceanic species (*Isograptus* and allies) were absent, but gradually return during the following transgressive phase, heralded by *Pseudotrigonograptus*. It is noted that the stratigraphic columns of Mu *et al.* (1979: opp. p. 12) show the appearance of limestones in otherwise shaly sections at the Zone of '*Azygograptus suecicus*'.

3. In Utah Braithwaite (1976) described the graptolite sequence from an outer cratonic site where trilobite-bearing rocks are often interbedded with greenish graptolitic shales. The lithology of these shales is unlike that of typical black, fissile graptolitic shales of 'geosynclinal' type. Again, our Middle Arenig interval is certainly present, with what is probably true *Phyllograptus* associated with pendent didymograptids showing isograptid development, and therefore referable to *Didymograptus (Didymograptellus).* Pendent graptoloids reappear in the Llanvirn Kanosh Shale. Between the two pendent-bearing intervals lie the Wahwah and Juab Limestone Formations. The younger of the two, the Juab Limestone, has only two species of graptolites, and one of these (identified with *Didymograptus nitidus* (Hall) by Braithwaite) has a described development which shows it to be a *Xiphograptus* species. Furthermore other extensiform didymograptids with development described by Braithwaite from the upper Wahwah Limestone Formation would now be classified in *Xiphograptus*; a form occurring just below the Juab Limestone, incorrectly described as *D. extensus* by Braithwaite, may be identical to *Xiphograptus formosus svalbardensis* (Archer & Fortey) from Spitsbergen. Finally, what is identified as *Phyllograptus anna* (Braithwaite 1976: 32–35), which occurs with the *formosus*-like species, is clearly a *Pseudophyllograptus* from its development, a genus that makes its reappearance above the *D. bifidus* interval in Spitsbergen. So there seems to be some evidence of a very thin interval at the top of the Wahwah Limestone representing the Upper Arenig. No isograptids are present at all. There may still be a considerable disconformity between the Wahwah and Juab Limestones but the graptolite faunas of the latter are not sufficient to resolve this problem. The trilobites from the Juab are of Hintze's (1953) Zone L, which we have good reason (Fortey 1980*a*: 13–15) to correlate with the basal Whiterockian V_4b (youngest) trilobite fauna from Spitsbergen. Hence the entire Valhallan interval has to be accommodated within the upper 17 m of the Wahwah Limestone, compared with virtually a third of the Valhallfonna Formation in Spitsbergen. By comparison with zones above and below it would be very attenuated, and this too would be consistent with the idea of a Valhallan regression.

These three examples have been discussed in detail because they occur in areas which were on three different plates in the early Ordovician, and which were clearly affected simultaneously by an event in widely separated parts of the Pacific Province. What happened in each area is consistent with the idea of the Valhallan regression. Note that faunas in true oceanic sites were unaffected by the regression. For example in the oceanic facies contemporaneous with the Wahwah and Juab Limestones, now in the allochthonous Vinini Formation (Ross & Berry 1963) of Nevada, there is a good succession of *Isograptus* species. Spitsbergen appears to be unique in recording a rich, mixed shelly/graptolitic fauna across this interval in the Bathyurid trilobite Province.

The same event should have affected the Atlantic Province, but the more indirect basis for correlation should always be considered first. Nonetheless there is evidence of a similar event at a similar time. For example, the 'Orthoceras Limestone' interval between the Lower and Upper Didymograptus Shales in the Oslo region falls exactly where we would expect our regressive phase. Furthermore the fauna described by Spjeldnaes (1953) from the top of the Lower Didymograptus Shale at Slemmestad includes both *Didymograptus hirundo* and *Pseudotrigonograptus* (see p. 250). In south Wales work in progress by R.A.F. and R. M. Owens shows that there is a change in facies at the Arenig–Llanvirn boundary which introduces a number of relatively shallow water trilobite genera, such as *Ectillaenus,* in light-coloured shales, into a sequence otherwise dominated by black mudstones and turbidites, with 'open ocean' trilobite faunas.

Rhabdosome morphology, development and terminology

The terminology currently used in graptolite description has evolved over many years. The early work of Hall (1858, 1865), Lapworth (1873, 1875) and Nicholson & Marr (1895) was refined by Elles & Wood (1901–18), who evolved a terminology which was used by almost all subsequent workers and which forms the basis of that used today. Detailed morphological studies of rhabdosomes isolated from their matrix late last century (Holm 1890, 1895, Wiman 1895, 1901) and this century (Kraft 1926, Bulman 1932–36*a*, 1944–47, Kozlowski 1949, and several papers during the last two decades) has led to a refinement or revision of many terms used to describe the morphology, structure and development of the rhabdosome, together with the addition of many new ones. Bulman (1955, 1970) has systematized terminology in the *Treatise* and provided the basis for terminology used in the present work.

Throughout this paper, the term **dichograptoid** is used as an informal term to describe graptolites with dichograptid grade of organization, but without phylogenetic connotations.

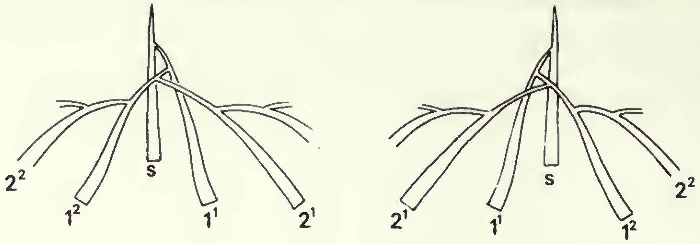
It was perhaps inevitable that the renewed attention here directed towards the proximal region of the dichograptoid rhabdosome should result in the necessity for a revision of Bulman's scheme of terms to describe the proximal end. In view of the importance here attached to development type, mode, and proximal structure it is proposed to isolate these three concepts and redefine them. The new morphological information now available has required a revision and redefinition of Bulman's classic sequence of development types and their supposed phyletic relationships. For much the same reason it is proposed to revise Bulman's system of thecal notation, and a reference frame for orientation of the rhabdosome is proposed, together with a system for stipe notation.

Developmental types and their nomenclature

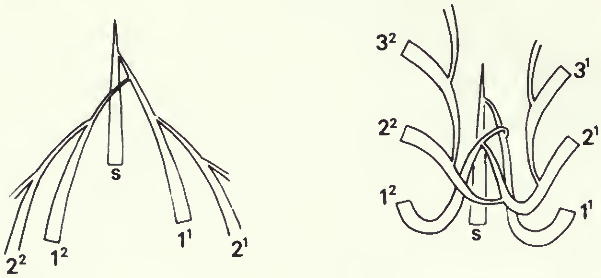
Systematic study and classification of the various kinds of early astogenetic structure and development have been very largely the work of Bulman. He incorporated the work of earlier authors, particularly Holm (1890, 1895), Wiman (1893, 1895) and Elles (1922), with his own studies of Swedish etched specimens prepared by Holm into a scheme of 'progressive changes in the proximal end of the graptolite rhabdosome' (Bulman 1932 and, somewhat revised, 1936*b*, 1970: fig 49). His scheme of development types incorporated not only thecal budding sequence but also structural features of the proximal region, such as directions of growth of proximal thecae and their arrangement with respect to the sicula.

The term 'proximal development type' is here used to refer only to the sequence of budding of proximal thecae. Among Graptoloidea, the first two, three, four or more thecae may alternate in origin by progressive postponement of formation of the first dicalycal theca of the rhabdosome. In dichograptoids the dicalycal theca is either th1^1 (Fig. 4c; dichograptid type of Bulman) or th1^2 (Fig. 4a–b; isograptid type of Bulman). The diplograptids, not part of this study, are here considered briefly since any overall scheme of development types must incorporate them. In the early forms theca 2^1 is dicalycal but in many later forms the dicalycal theca is some later theca or else dichotomy never takes place at all and thecae alternate throughout the rhabdosome (aseptate forms). For purposes of the present discussion, we recognize two types among diplograptids; in the first (diplograptid 1) th2^1 is dicalycal (Fig. 4d); in the second ('diplograptid 2', which itself probably includes several distinct types) the dicalycal theca is th2^2 or a later theca, or the rhabdosome is aseptate. The four development types are listed in Table 1. Uniramous forms such as *Azygograptus* and *Monograptus* are thought to have been derived from biramous forms by loss or suppression of the initial dichotomy, and may warrant recognition as a discrete development type.

Development of the dichograptoid rhabdosome has been examined in detail by Cooper & Fortey (1982) and related to the early astogenetic development of dendroids. The dichograptid type of development, in which theca 1^1 is dicalycal, was found to be rare among dichograptoids and largely confined to pendent didymograptids of the *D. artus* group of Llanvirn age. The name dichograptid type therefore seems inappropriate. Furthermore it comprises a single stage, based on the Welsh *Didymograptus 'bifidus'*, known as the *bifidus* stage. However,



a isograptid, dextral b isograptid, sinistral



c artus type, dextral d diplograptid (1) type, dextral

Fig. 4 Thecal diagrams to illustrate the terms *dextral, sinistral, right-handed* and *left-handed*. a, Isograptid development type with right-handed origin of th1^2 (and left-handed origin of 2^1) dextral mode of development (e.g. *Didymograptus (Expansograptus) extensus*). b, Isograptid development type with left-handed origin of th1^2 and sinistral mode of development *(Isograptus caduceus imitatus)*. c, *artus* development type with right-handed origin of th1^2 and dextral mode of development *(Didymograptus artus)*. d, diplograptid (1) development type with left-handed origin of th1^2 and dextral mode of development *(Glyptograptus austrodentatus)*.

Didymograptus bifidus, sensu stricto, is here shown to have th1^2 dicalycal, and the Welsh '*bifidus*', with dicalycal th1^1, represents a different species requiring a new name. The name ***artus* type** has therefore been proposed to replace dichograptid type and is used in this work.

All stages in which th1^2 is dicalycal are collectively referred to by Cooper & Fortey (1982) as the isograptid type of development, which is found to be dominant among the dichograptoids. The leptograptid type of Bulman (1970) with dicalycal th1^2 was synonymized with the

Table 1 Development types proposed here compared with those of Bulman (1970).

Dicalycal theca	Development types proposed here	Development types of Bulman (1970)
th1^1	1. *artus*	1. dichograptid (*bifidus* stage) 2. pericalycal (Glossograptina)
th1^2	2. isograptid	3. isograptid (*minutus, extensus* and *gibberulus* stages) 4. leptograptid
th2^1 th2^2 or later	3. diplograptid (I) 4. diplograptid (II)	5. diplograptid

isograptid type and the *minutus* stage was also referred to the isograptid type following Bulman (1970).

The various stages within the two main development types found in dichograptoids, which were thought to represent a progressive series by Bulman (1936*a*, 1955), have received decreasing emphasis in recent years as it has become increasingly unlikely that they represent transitional stages in the evolution of the isograptid from the dichograptid type as originally proposed (Bulman 1932, 1936*a*). In 1970 Bulman suggested that the two main types stood in parallel rather than serial relationship and that there is little purpose in attempting to distinguish the various stages within each type. In any case, the morphology of the rhabdosome rarely allows them to be determined with precision. Most recently, the isograptid type of development of the rhabdosome is claimed by Cooper & Fortey (1982) to be the primitive type for all Graptoloidea and to have been derived directly from the Dendroidea by suppression of bithecae. The *artus* and diplograptid development types, on this hypothesis, must therefore have been derived from forms in which theca 1^2 is dicalycal. An ancestor with isograptid development has long been suggested for the earliest diplograptids by Bulman (1936*a*: 94, text-fig. 30) and more recently by others (e.g. Jenkins 1980). In this paper we suggest that the Llanvirn pendent didymograptids of the *artus* group were derived from an Arenig pendent form with isograptid development.

In summary, we recognize two types of development in dichograptoids; the *artus* type and the isograptid type. No stages are distinguished.

Proximal structure and its nomenclature

The second concept employed in Bulman's classification of the various kinds of proximal development is the growth directions and arrangement of proximal thecae, here referred to as 'proximal structure'. The distinction between the leptograptid and isograptid types of Bulman (1970: fig. 49), assuming that the leptograptid type has th1^2 dicalycal, is essentially based on the horizontal, rather than downward, growth of proximal thecae. Thus it is based on proximal structure, rather than on development type as defined here. In terms of development type, we regard it as identical with the isograptid type. There is great variety in proximal structure which, among the dichograptoids at least, holds much hope for deciphering phylogeny.

The terms streptoblastic and prosoblastic (Bulman 1963) refer to features of proximal structure, as do the terms pericalycal and platycalycal (Bulman 1968). The 'pericalycal type' of development was the term used by Bulman (1970) for the Glossograptina, which have th1^1 dicalycal and a pericalycal arrangement of proximal thecae. We would regard the glossograptines as of *artus* development type and with pericalycal structure. In fact, any of the other types of development would tend to impede the formation of pericalycal structure. However, reassessment of the glossograptines in the light of Finney's (1978) comments is needed.

The terms right- and left-handed refer to features of proximal structure and need clarification. They were first introduced by Stubblefield (1929) for describing the development of *Adelograptus hunnebergensis* and *Clonograptus tenellus*: 'One of the primary stipes may cross the sicula, either to the right or to the left-hand side, the sicula [in reverse aspect] is then for purposes of description termed respectively, right- or left-handed'. Right- and left-handed are commonly used to indicate the origin of the dicalycal theca (e.g. Bulman 1932: 5; 1970: V33, V75), for other proximal thecae (Bulman 1970: 77), or simply for 'development of the early thecae' (Bulman 1963*a*: 276). It should be noted, however, that Bulman used the terms in the sense opposite to that of Stubblefield, i.e. right-handed to Stubblefield was left-handed for Bulman, who sometimes used 'biologically left-handed' to make the distinction clear. It is in Bulman's sense that the terms have come to be accepted.

The terms do not necessarily relate to the direction of growth and orientation of a theca but but may merely reflect its origin. Hence in dicranograptids and other forms with diplograptid (1) development type, the origin of theca 1^2 is left handed but it grows around th1^1 and across the sicula in a clockwise or dextral sense, in the same way as in dichograptids where the origin of this theca is right-handed.

Thus there is a need for two sets of terms relating to mode of development. **Right-** and **left-handed** are retained here to indicate the origin of a theca, that is whether it arises on the (biologically) right or left side of its parent theca. In the proximal part of the rhabdosome, this is determined (as used by Bulman) with respect to the sicula (Fig. 4), but after the first dichotomy it is determined with respect to the parent theca. Thus in *Phyllograptus typus* (Fig. 75, p. 282) the origin of theca 1^2 is right-handed (on th1^1), the origin of th3^1 is right-handed (on th2^1) and the origin of th3^2 is left-handed (on th2^2). In normal budding along a stipe thecae originate on the dorsal side of their parent thecae, and the terms right- and left-handed are not applicable.

The terms dextral and sinistral are proposed to describe the sense of rotation of a theca which grows from one side of a bifurcation to the other and is independent of whether it is right- or left-handed in origin. **Dextral mode** of development indicates that the first 'crossing canal', the proximal part of theca 1^2, grows around in a dextral or clockwise sense with respect to the sicula; th1^1 will thus lie to the right of the sicula when seen in reverse aspect (Fig. 4a). This is by far the most common mode of development in graptolites. In the **sinistral mode** of development, th1^2 grows around in a sinistral or anticlockwise sense so that th1^1 lies to the left of the sicula in reverse aspect (Fig. 4b). Examples are few and include *Oncograptus* (Bulman 1936*b*), the Glossograptina, and *Isograptus imitatus* together with several dendroids (including *Dictyonema flabelliforme, Clonograptus tenellus,* and *Adelograptus hunnebergensis*; Stubblefield 1929) in which development mode appears to be arbitrarily sinistral or dextral. The terms can also be applied to subsequent dichotomies where a sense of torsion is imparted by the first daughter theca of a dicalycal theca and relates to the predicalycal theca. Thus in *Tetragraptus (T.) phyllograptoides triumphans* (Fig. 5a, b), and in fact all tetragraptids, the second order dichotomy on stipe^1 side is sinistral whereas that on the stipe^2 side is dextral.

Thecal notation

Bulman's (1936*a*: 32) system of trinomial notation for thecae in the proximal region of the rhabdosome was derived from the binomial nomenclature introduced by Elles (1897: 189–190)

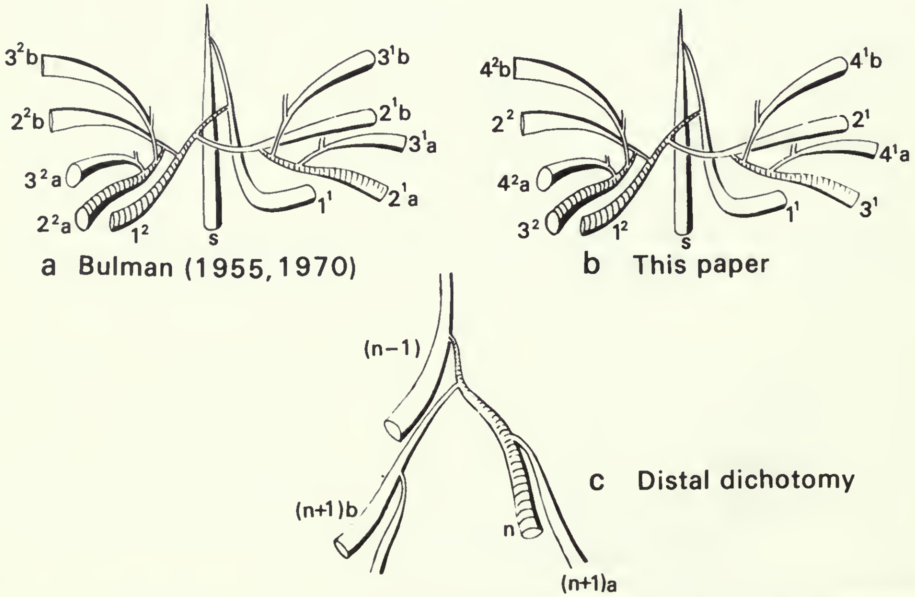


Fig. 5 Thecal diagrams to show budding sequence and thecal notation in proximal and distal regions of a branching dichograptid. a, Bulman's (1955, 1970) scheme for the proximal region. b, Scheme proposed in this paper for proximal region. c, Scheme for a distal dichotomy. Diagrams a and b are based on *Tetragraptus (Tetragraptus) phyllograptoides triumphans* described in this paper, p. 201. Diagram c is based on Dichograptid sp. *A* of Skevington (1965). Dicalycal thecae striped.

and designed to accommodate those tetragraptid and phyllograptid rhabdosomes whose development was then known. The scheme used in the *Treatise* (Bulman 1970: V74) is basically the same one (Fig. 5a). In 1936, prior to the concept of the dicalycal theca, it was thought that the third-formed theca of the tetragraptid rhabdosome, th2^1 (and the fourth formed theca, th2^2) split equally into two; thus Bulman (1936*a*: 32) states that it 'divides and opens to the exterior as two separate thecae which are called th2^1a (on the reverse side) and th2^1b (on the obverse side)'. Although it was later realized that th2^1a, rather than being a sister theca to th2^1b, is in fact a daughter theca budded off from th2^1b (Bulman 1955: fig. 39, 3; 1970: fig. 53), nonetheless the original nomenclature was retained. Thus the designations th2^1a, th2^1b do not denote two daughter thecae of a dicalycal parent theca, but thecae whose apertural regions form part of stipes a and b respectively. The scheme thus reflects the position in a thecal series (stipe) of the apertural portion of a theca, rather than its strict order of budding. Theca 2^1b is the first theca of stipe ^{1}b and the first theca of stipe ^{1}a is the subsequently budded th2^1a (Fig. 5a); th3^1a, 4^1a etc. are successively budded thecae of stipe ^{1}a. Since thecae 1^1 and 1^2 do not form part of the second order stipes in the species studied by Bulman (*T. bigsbyi* and *'Phyllograptus' angustifolius*) they needed no a or b connotation.

Bulman's system has the merit that thecae can be labelled from their position in a thecal series without knowing their budding sequence. Against this it can be said that thecal notation is used mainly where budding sequence is known, often to describe the budding sequence specifically, as in discussions of the various development types. In these instances it seems more logical that nomenclature should reflect the budding sequence rather than the position in the stipe. The budding sequence is certainly a more fundamental and conservative character than the position a theca holds in a stipe, and the system fails for such forms as *Phyllograptus, sensu stricto* (here defined to exclude *'Phyllograptus' angustifolius,* = *Pseudophyllograptus* gen. nov.) where the initial two thecae, th1^1 and 1^2, form the first thecae of stipes ^{1}a and ^{2}a respectively rather than lying medially between them as in *T. bigsbyi* and *P. angustifolius*.

A further, and possibly more serious, objection to the present system lies in the difference in notation used for proximal and distal dichotomies. It is claimed elsewhere (Cooper & Fortey 1982) as a general rule that in branching dichograptoids, division of the stipe in distal dichotomies is achieved by a repetition of the process by which division takes place in the proximal region, i.e. of the initial development. If this rule holds, it is obviously desirable that the one notation system should be applied at all dichotomies. The current notation of thecae of a distal dichotomy differs from that used for thecae of a proximal one, as a comparison of Bulman's (1970) figs 64.1 and 64.2 shows.

It is therefore proposed to change to a system which reflects the sequence of thecal budding and to use it for proximal development and for all subsequent dichotomies. In the new system the daughter thecae of a dicalycal theca, th n, are labelled (n + 1)a and (n + 1)b. In the original system, 'a' was used for stipes (and thecae) developed on the reverse side of the rhabdosome and 'b' for stipes on the obverse side. Although this scheme has proved to be generally satisfactory it could not be applied to distal dichotomies of rhabdosomes in which the proximal region is not preserved. It is therefore proposed to denote the second budded theca (and subsequent stipe) of a dicalycal parent, 'a', and the first budded theca, 'b', consistent with the earlier system. The old and new systems of nomenclature are given for the thecal diagram of *Tetragraptus (T.) phyllograptoides triumphans* in Fig. 5a, b. By extension, the scheme can be applied to subsequent dichotomies, e.g. a dicalycal theca 4^1a would produce daughter thecae 4^1a^1 and 4^1a^2, and so on. For isolated distal fragments (Fig. 5c), a dicalycal theca n produces first a daughter theca (n + 1)b which gives rise to stipe b and next a second daughter theca (n + 1)a from which stipe a is derived, that is, the notation shown in Bulman's (1970) fig. 64.1 for a distal fragment of Dichograptid sp. *A* of Skevington (1965).

When we turn back to the proximal region and examine the notation of thecae of the initial dichotomy, that giving rise to the two primary stipes, we find that the first- and second-formed thecae are labelled 1^1 and 1^2 respectively. If the new scheme were applied to these they would be relabelled th1 and th2 and the superscript 1 and 2 would be introduced only for the daughter thecae of the first dicalycal theca, th1^2 (or 1^1 in *artus* type development), and their descendants.

Such a change would alter the nomenclature of all subsequent thecae and make the comparison of the old and new systems difficult and confusing. It would also require revision of the schemes used for diplograptids, dicranograptids, etc., now so well established in the literature, and generate an unwarranted upheaval in conventional usage. It is therefore proposed to leave notation of the first dicalycal theca, and its parent theca in the case of isograptid type developmental forms, as at present and introduce the new notation from the second dicalycal theca(e) onwards. For species with *artus* type development there is no change in nomenclature.

Later astogenetic development – dichotomy and branching types. In classification of multistiped dichograptoids much weight has been placed in the past on branching patterns and the number of terminal stipes. In discussing the multistiped forms from Spitsbergen, particularly those of the subfamily Sigmagraptinae nov., we have found it useful to discuss branching pattern in terms of the spacing and distribution of dichotomies throughout the rhabdosome. A number of descriptive terms have proved necessary.

Dichotomy is the process by which a stipe divides to produce two new stipes. All dichotomies appear to employ the same process of division, described by Cooper & Fortey (1982) as the isograptid type of stipe division. Dichotomies can be consecutive throughout the rhabdosome or delayed. In *consecutive dichotomies* only one theca separates successive dicalycal thecae and there is thus only a single theca between each branching node. Examples are *Tetragraptus bigsbyi* and *Dichograptus octobrachiatus*. In *delayed dichotomies* two or more thecae separate successive dicalycal thecae and branching nodes are thus more spaced out. A good, if somewhat exaggerated, example is *Laxograptus* [*Zygograptus*] *irregularis* redescribed here, p. 270.

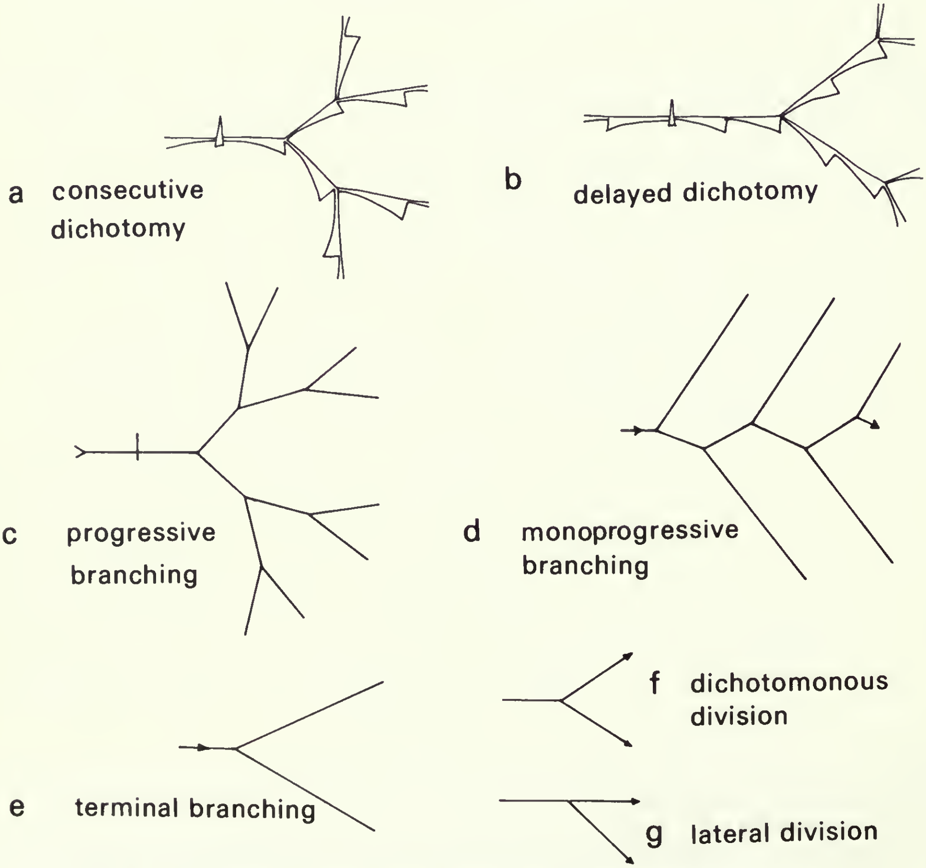


Fig. 6 Branching types and their nomenclature as followed in this paper.

Branching is of several kinds. *Progressive branching* is that kind in which two new branches are formed, each of which subsequently divides again. In *monoprogressive branching,* two branches are formed only one of which further divides, the other remaining undivided. Branching in *Loganograptus* and *Dichograptus,* for example, is of the progressive kind, whereas branching in *Goniograptus, Sigmagraptus, Pterograptus* and *Trichograptus* is of the monoprogressive kind. The term *terminal branching* can be used when neither of the two new branches further divides and they thus become terminal stipes of the rhabdosome. However, in discussion, it is often convenient to regard terminal branching as of the same kind as, but the final stage of, whatever branching type precedes it.

Two further terms are already in use and defined in the *Treatise* (Bulman 1970) and relate to the angle of divergence of the daughter stipes. *Dichotomous branching* is used where the two daughter stipes diverge symmetrically from the parent stipe and *lateral branching* where one daughter stipe continues the direction of growth of the parent stipe whereas the other diverges from it at an angle. The terms are a little unfortunate in that we now believe that both lateral and dichotomous branching are produced by normal dichotomy (i.e. by the isograptid type of stipe division) and both are, in that sense, dichotomous.

Stipe notation

Stubblefield (1929: 274 and footnote) extended his use of right- and left-handed to denote the primary stipes of *Clonograptus tenellus, Adelograptus hunnebergensis* and, by extension, any rhabdosome with a proximal dichotomy. However, a less ambiguous notation, derived from Elles' (1897) binomial thecal notation, has gained wide acceptance and is in general use today (e.g. Bulman 1970). It can be extended to denote stipes of the second, third, fourth, etc., orders by use of polynomials as shown in Fig. 7 and derives logically from thecal nomenclature. It should be noted that where a dichotomy (after the first) is of sinistral mode, the left-hand stipe (seen from above) is denoted b (or ^{2} depending on the order of dichotomy) and the right-hand stipe is denoted a (or ^{1}). Where a dichotomy is of dextral mode the left-hand stipe is denoted a (or ^{1}) and the right-hand stipe b (or ^{2}). Where mode of dichotomy is unknown, notation of the daughter stipe is arbitrary.

The term 'stipe' strictly speaking refers to a segment between dichotomies but it is convenient to leave definition of the term deliberately loose and to rely on context for precise meaning. The notation scheme provides a means for precise identification of individual segments. We see no reason why the one scheme cannot be applied to both lateral and dichotomous division since we regard both as resulting from the one, isograptid, branching process and thus to be of the same fundamental type.

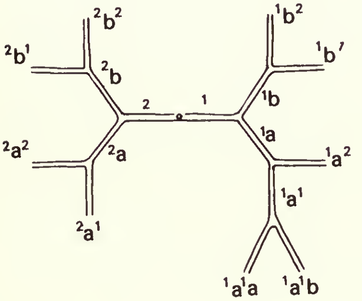


Fig. 7 Notation of stipes in a multistiped rhabdosome.

Orientation of the rhabdosome

It is useful, for purposes of description, to have a frame of reference for orientating the rhabdosome. The terms *dorsal* and *ventral, proximal* and *distal* are well established in reference to individual stipes, to individual thecae and to the rhabdosome itself. Terms for describing stipe attitude are also well known (Bulman 1970: fig. 38), but there appears to be no generally accepted overall frame of reference as has been established in other biological groups.

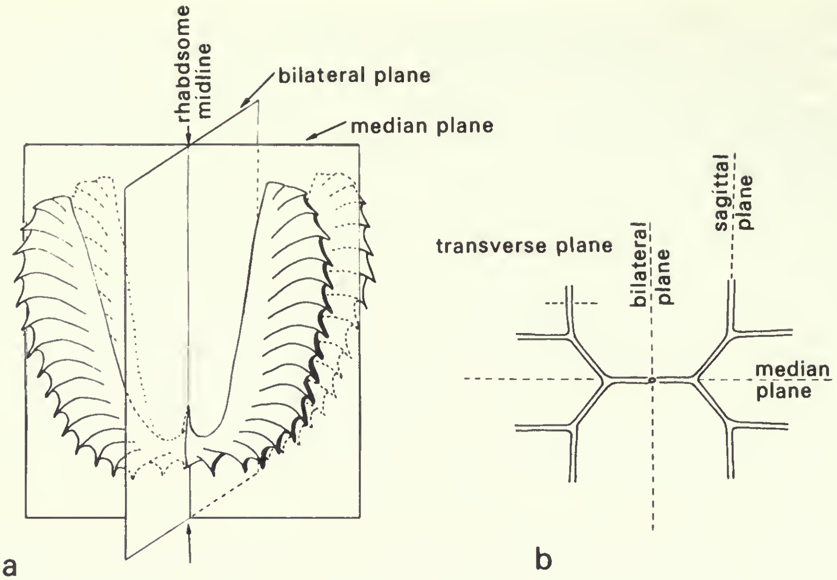


Fig. 8 Planes of reference of the rhabdosome. a, *Tetragraptus pseudobigsbyi* with the two principal planes of symmetry. b, a multistiped dichograptid (dorsal view) with planes of reference and symmetry.

The scheme proposed here (Fig. 8a, b) is primarily for convenience in description of the Didymograptina of Bulman (1970), but most of the suggested reference planes and axes can be applied to other suborders and to the Anisograptidae. Most dendroids, however, with their irregular branching characteristics and rhabdosome habit, defy attempts to impose planes, or axes, of symmetry on them.

For descriptive purposes the rhabdosome is usually orientated with the apex of the sicula (and nema) uppermost. The rhabdosome *midline* (the primary axis of symmetry) passes through the sicula and medially through the rhabdosome, from top to bottom (Fig. 8a). The plane containing the rhabdosome midline and the two primary stipes is here called the *median plane* of the rhabdosome; it is a plane of symmetry in rhabdosomes developed on both the didymograptid (and tetragraptid) and triograptid planes. In diplograptids it passes through the ventral midlines of the two thecal series whereas in Glossograptina it passes between the two thecal series themselves. The plane which lies normal to the median plane, and which also contains the rhabdosome midline, is the *bilateral plane* of the rhabdosome – the principal plane of symmetry in bilateral rhabdosomes. The third plane of reference, of course, is already referred to as the *horizontal plane.* The long axis of a stipe is generally referred to as the *stipe axis*; the plane normal to the stipe axis is here called the *transverse plane* of the stipe and the plane passing through the dorsal and ventral margins of the stipe, and containing the stipe axis, is here called the *sagittal plane* of the stipe. In Diplograptina, the sagittal plane coincides with the median plane of the rhabdosome and in many monograptids (*M. turriculatus, Cyrtograptus*) is the only plane (besides the horizontal plane) that can readily be applied.

Stipe expansion diagrams. We have used this method as a simple and graphical way of directly comparing different specimens and species of dichograptoids on a single diagram. It is more objective than the general statements about the form of stipes, rate of expansion and change in thecal length found in many descriptions. The graphs plot the width of a stipe, from its dorsal margin to the tip of the apertural denticle, against the thecal number (1, 2, 3 . . .) counted from the proximal end (Fig. 9).

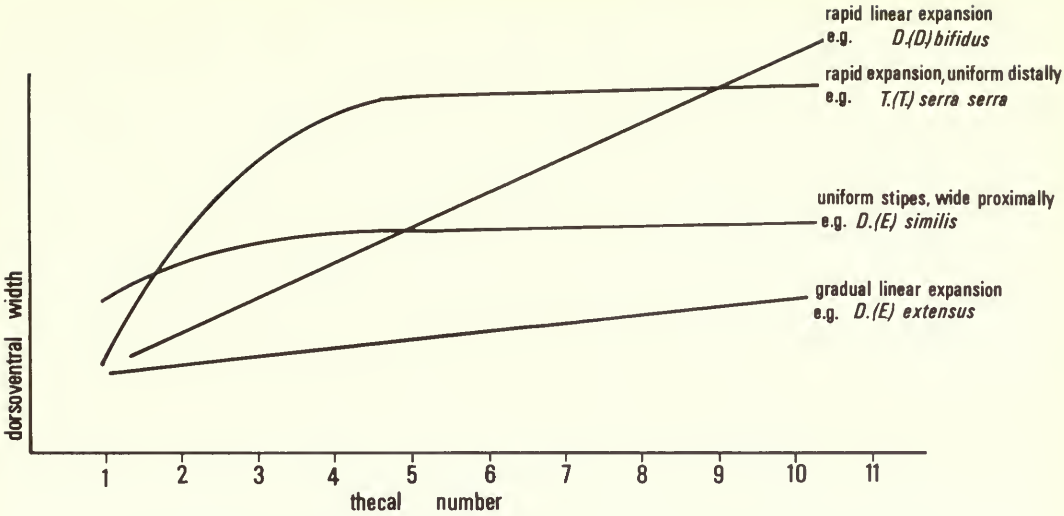


Fig. 9 Stipe expansion diagram with some characteristic expansion curves.

Different species within a given form genus tend to have characteristically different shapes on the stipe expansion diagrams. Variation can be simply assessed by plotting stipes from several specimens in a population on the same diagram. We have found this method of particular use in evaluating the specific status of rather undistinctive species of the subgenera *Didymograptus (Expansograptus)* and *Didymograptus (Didymograptellus)*. In general the *shape* of the expansion curve tends to be rather constant within a species, but the absolute value of, for example, maximum stipe width can be highly variable (see *Tetragraptus serra serra*, p. 196). The method has the advantage that the shape of the expansion curve can still be deduced when some thecae are poorly preserved and when the vagaries of preservation make some individual thecae relatively wide or narrow. Some species have growth increments which result in regular expansion diagrams to which a straight line regression may be fitted with correlation coefficients in excess of 0·9. For the sake of clarity it is often easier to compare sets of such regression lines derived from a population of rhabdosomes, although the intercept does not necessarily correspond with the proximal width of the stipe. Non-linear growth is typical of other species, and the general shape has been emphasized using a flexible curve to ‘average’ the points. Note that this method includes no measure of thecal *density*, usually recorded as number of thecae corrected for 10 mm: in theory it is possible to get identical expansion diagrams from two species with very different thecal spacing. Once proximal end characters, general thecal and rhabdosome form, and thecal spacing have been described, the expansion diagram neatly encapsulates many of the features of the distal stipes, and facilitates direct comparison of type series with specimens to hand.

Other terms

Most other terms used are already in general usage but the following need clarification. *Growth lamelli* and *growth lines* both refer to overlapping half-rings (fusellar rings or fuselli) of the periderm and are visible in transparent isolated rhabdosomes. Much of the isolated material from Spitsbergen is too heavily carbonized to be rendered transparent by bleaching but nonetheless shows fine striations on the outer surface of the rhabdosome which can be traced under camera lucida and indicate the growth directions of thecae. Although the striations proved to be always parallel with fuselli, where both could be observed, the spacing of the striations was found to be twice as close as that of fuselli (e.g. in *Xiphograptus formosus svalbardensis*). It is important therefore to distinguish them from true fuselli and they are here called *growth striations*. They are extremely useful for determining growth direction and development of the proximal region, for example in *Phyllograptus typus*, but do not necessarily represent individual increments in the fusellar tissue.

Another term we have found useful refers to the arch formed by the ventral walls of th2^1 and th1^2 in the isograptid development type. It is usually a conspicuous feature and a good guide to isograptid type development even in strongly flattened material. It is here called the *isograptid arch*. The symmetrical arrangement of the sicula and first theca, characteristic of isograptids and approached by many species with isograptid development, is referred to as *isograptid symmetry*, following Cooper (1973).

The term **fornix** refers to the arched strut which stands in place of the interthecal septum in the axial region of *Phyllograptus*. The wide opening between thecal series is termed the **fornical foramen.**

Unless otherwise specified stipe width and thecal width are measured in the sagittal (dorso-ventral) plane.

Principles of dichograptoid classification

There appears to be a degree of consensus in the papers of graptolite workers over the last few years that the only satisfactory classification of the group will be one based on their inferred phylogeny (Rickards, Hutt & Berry 1977; Bouček 1973). The historical problem has been that the genera or families originally proposed for graptolites have often been based on the grade of organization of the rhabdosome, especially the number and arrangement of stipes. In a series of papers Bulman (e.g. 1936*a*, 1963, 1970) has argued that in many cases the particular grade of organization found in a graptolite rhabdosome may be polyphyletically derived. The 'genera' in use were often stratigraphically useful in a crude way, and had the advantage of being readily recognizable, but may include clusters of species whose closest relatives lie not within the same form-genus, but in some other form-genus of an equally polyphyletic nature. But over the last three decades various other genera have been proposed (on our estimate perhaps half of those used in the 1970 *Treatise*), which are explicitly defined in terms of characters of presumed phylogenetic significance – they are believed to be 'true' phylogenetic concepts in which every species included in the genus is presumed to be more closely related one to another than to any species in another genus, and to be all derived from a common ancestor. Thus, for example, *Aulograptus* Skevington 1965 is of *Didymograptus* grade of organization, but defined as a phylogenetic unit by having climacograptid thecae. This leaves graptoloid classification in an unsatisfactory, hybrid state. The progress towards solution of some of these problems was well put by Bulman & Rickards (*in* Bulman 1970: 150) in discussing monograptids: . . . 'the hope remained that from the portmanteau genus . . . various soundly based genera could progressively be extracted as investigation of different species provided the opportunity'. The important phrase here is 'soundly based'. The recognition of the polyphyletic nature of some of the long-used graptolite genera has led to the proposal of new 'genera' by some authors which are every bit as polyphyletic as their more encompassing predecessors.

This problem is nowhere more acute than in the dichograptoids (= Dichograptidae of Bulman 1970). Bulman (1955) suggested the different phylogenetic routes by which a rhabdosome of *Tetragraptus* or *Didymograptus* organizational grade could be derived. His diagrammatic representation would suggest that not only are most dichograptoid genera polyphyletic concepts, but also that the family as a whole is probably polyphyletic – it is the taxonomic expression of a stratigraphically-based anagenetic grade of evolution, meaning little more than the statement 'early graptoloids tend to have several stipes'.

There have been a number of attempts to define phylogenetically meaningful groups in the dichograptoid plexus. Mu (1957) erected a family Sinograptidae for a number of genera paralleling the dichograptoid 'genera' on stipe number and attitude, but united by a presumed shared, derived character (strong prothecal folds) which reveals an underlying phylogenetic connection. Most graptolite workers would probably accept that the Sinograptidae is a phylogenetic entity. As far as the old form genera like *Didymograptus* and *Tetragraptus* are concerned several genera have been proposed to split up these large assemblages of species. In

Didymograptus there are four such – *Expansograptus* Bouček & Přibyl 1951, *Corymbograptus* Obut & Sobolevskaya 1964, *Acrograptus* Tzaj 1969 and *Aulograptus* Skevington 1965. The first three of these are simply formal upgradings of Elles & Wood's (1901) informal division of *Didymograptus* based on stipe attitude. There is little to suggest that this is genuinely a phylogenetically important character, and there *is* evidence to suggest the contrary. For example, we describe a group of extensiform graptolites in this paper (p. 289) which on stipe attitude definition should belong to *Expansograptus* or *Acrograptus* but which have a proximal end structure which shows them to be unrelated to the type species of either of these 'genera'. The proximal end structure serves to define a phylogenetic entity, but within this group stipe forms vary from extensiform (i.e. *Expansograptus*) to strongly declined (i.e. *Acrograptus*), which shows how mutable such general characters can be (and the same plasticity is shown by the sinograptids). The indications are, then, that the current definition of subgroups within the old genus *Didymograptus* would introduce the possibility of more polyphyly – in effect, would compound the traditional problem. The exception is *Aulograptus*, which as has been said has a derived character (climacograptid thecae) which is probably not polyphyletic. However, the other names are validly proposed, and we here employ them where appropriate as subgenera of the form-genus *Didymograptus*, based on the characters of their nominated type species, of which stipe attitude is not regarded as specially important. Particular problems associated with this procedure are given in the systematic treatment (pp. 218, 231, 239). The same arguments can be repeated for the subdivision of the form-genus *Tetragraptus*. In all these dichograptoids the phylogenetic validity of a genus depends on the recognition of a character or characters which may reasonably be supposed to indicate its monophyly (synapomorphy). Too little is known of detailed dichograptoid structure from isolated material to make more than a start in the direction of phylogenetically-defined genera.

There are no invariable rules about which characters shall be taken as signifying phylogenetic connections above the species level. However, we are clear in our assertion that the characters of the proximal end, particularly the sicula and first three or four thecae, are important in the discrimination of monophyletic groups. This can be justified both from a theoretical standpoint, and in the light of our own experience with isolated material.

1. It is reasonable to regard astogeny – the development of the colony – as a special case of ontogeny. Gould (1977: 269) implicitly makes this assumption in his discussion of thecal elaboration, and the same principle is accepted in coral and bryozoan work. From a phylogenetic standpoint the early astogeny may be treated in a broadly similar way to the embryological history of the single organism, and will be subject to von Baer's 'laws of development' (Gould 1977: 56). This is not to assert that the proximal development was immune from natural selection – the fact that fundamental changes in proximal structure do occur shows that this was not so – only that graptoloids *sharing distinctive proximal end characters will belong to a monophyletic group*.

2. Another way of showing this is to demonstrate that the same grade of rhabdosome organization may be reached by two independent lineages and that this independent origin can only be revealed by studying the proximal end characters. The proximal end structures in this case are homologous, whereas the rhabdosome structure as a whole is a parallelism. The phyllograptid rhabdosome is an excellent example. At first sight the four-stiped, scandent habit may seem peculiar enough for its monophyletic origin to be certain. Yet we show here that there are two totally different proximal structures with mature phyllograptid habit. One of these, that described by Bulman (1936*a*), is consistent with other dichograptoids. The other is different from most dichograptoids, but can be compared with a group of species with extensiform didmograptid habit (here put in *Xiphograptus* gen. nov.), typified by a short sicula with a long virgellar spine, and an antivirgellar origin of th1^1. There are only two possibilities:

(a) that the phyllograptid habit is the phyletic character and the proximal end structure independently derived, or

(b) that the proximal end structures are indicators of phyletic relationships, and the phyllograptid habit independently derived.

If we adopt the first we have to accept the extremely unlikely proposition that at an early stage of growth, *before* the defining character of the rhabdosome has been initiated, two quite different but closely related free-living growth stages have no close phyletic relationship with identical growth stages of other graptoloids. If the second explanation is accepted, then the only concession that has to be made is to allow the phyllograptid rhabdosome organization to be polyphyletic, in the same way as scandency in general, or periderm reduction. The second alternative is favoured, indeed Bulman (1936*b*: 44) suggested that '*Phyllograptus*' could have arisen on several 'lines of descent' although for reasons different from those put forward here.

Families and subfamilies

If the basis of classification outlined in the previous section is acceptable, it provides a method for the identification of natural groups above the genus level. For example true *Phyllograptus* and *Xiphograptus* are more closely related one to another than to any dichograptid since they share distinctive proximal characters. Hence in terms of proximal structure the family Phyllograptidae of Lapworth, 1873, should contain these two genera, but exclude the superficially comparable *Pseudophyllograptus*. This definition of the family Phyllograptidae contrasts with that of Mu (1957) who included both *Phyllograptus, sensu lato,* and *Pseudotrigonograptus,* on the basis of their multiserial scandent habit.

Similarly, within the Dichograptidae it should be possible to define groups of genera (subfamilies) with comparable proximal end structure, which may span the whole gamut of stipe number and arrangement. Sigmagraptinae subfam. nov., we suggest, is one such grouping, and others should be identifiable when more isolated material has been described. We cannot accept the elevation of the old 'form genera' *Didymograptus, Tetragraptus,* etc., to family status, such as has been used by Mu *et al.* (1979), because this is simply an upgrading of the old polyphyletic classification. Such units have little to recommend them stratigraphically, and nothing to recommend them phylogenetically.

Ultimately the dichograptid subgroups, and the Phyllograptidae, should 'root back' into the Anisograptidae. We see it as inevitable that, at least for the time being, the Anisograptidae should be retained as a paraphyletic stem group for subsequent graptoloid evolution, although much is likely to be gained from detailed studies of anisograptid development to detect the beginnings of those features which were to characterize the main lines of graptoloid evolution in the Arenig and younger rocks.

Systematic descriptions

Order **DENDROIDEA** Nicholson, 1872

Genus ***CLONOGRAPTUS*** Hall, 1873

TYPE SPECIES. *Graptolithus rigidus* Hall 1858.

Clonograptus trochograptoides Harris & Thomas 1939

Pl. 2, fig. 2

STRATIGRAPHIC RANGE. Lower part of Olenidsletta Member, V_1b, 22 m from base, early Arenig, late Bendigonian.

MATERIAL. PMO NF2792, NF2795.

DISCUSSION. This very robust *Clonograptus* species was originally described from Bendigonian rocks in Australia, and this is its first record other than the description of the type by Harris & Thomas (1939). No other Arenig *Clonograptus* (e.g. *C. flexilis* Hall) has so short and dense proximal branching, except *C. norvegicus* Monsen 1937. In that species the dichotomies are very irregular, and rather appear to give rise to a series of subordinate stipes from major, thicker stipes (Monsen 1937: pl. 20); the habit is generally lax and flexuous. Our specimen does not attain the size of the holotype figured by Harris & Thomas, but in our experience

Clonograptus can be variable in the ultimate number of dichotomies, and there seems to be no reason to suppose any specific difference in this case.

Order **GRAPTOLOIDEA** Lapworth, 1875

DISCUSSION. Classification above the generic level used here differs from that adopted in the *Treatise* (Bulman 1970) in several respects. The Family Dichograptidae is redefined using characters of the sicula and early development in combination with rhabdosomal features. It comprises three subfamilies, Dichograptinae, Isograptinae and Sigmagraptinae, discussed below. The new definition of Dichograptidae excludes those forms which have a virgellar spine on the sicula and in which theca 1^1 originates and grows on the antivirgellar (dorsal) side of the sicula, namely the genera *Phyllograptus* Hall, *sensu stricto,* and *Xiphograptus* gen. nov. These two genera are here grouped in the family Phyllograptidae Lapworth 1873.

Other families that appear to be phylogenetically well based have been mentioned in our discussion of the principles of dichograptid classification, and include Sinograptidae Mu 1957 and Abrograptidae Mu (*in* Mu & Lee 1958). Discussion of the relationship between all these families at higher level, and classification between the ranks of family and order, is beyond the scope of this paper. The informal term 'dichograptoid' is used for convenience in discussion for Dichograptidae + Phyllograptidae, i.e. the Dichograptidae of Bulman 1970.

Family **DICHOGRAPTIDAE** Lapworth, 1873

DIAGNOSIS (revised). Development platycalycal, of isograptid or, rarely, *artus* type, and dextral or, rarely, sinistral; virgellar spine not present on sicula, theca 1^1 originates and develops on ventral side of sicula; rhabdosomes generally have bilateral symmetry; all dichotomies employ isograptid division; dicalycal thecae throughout rhabdosome are separated, in budding succession, by one or more unicalycal thecae; dichotomies consecutive or delayed, branching progressive or monoprogressive; stipes usually uniserial, rarely biserial, triserial or quadriserial. Thecal form usually simple, rarely of climacograptid type.

DISCUSSION. Bulman's (1959, 1970) division of the Dichograptidae into the sections Goniograpti, Temnograpti, Schizograpti, Dichograpti, Tetragrapti and Didymograpti was a polyphyletic generic grouping of convenience – revealed clearly in his diagram (1970: fig. 75) showing suggested phylogenetic relationships among some dichograptid genera. In admitting the arbitrary nature of the sections, he stated (1970: V104) that 'no satisfactory subdivision of the large and varied family Dichograptidae on a formal subfamilial basis is yet possible.' It is our belief that although morphological information on the structure and development is lacking in many genera, we now know enough to make a start on regrouping species and genera into units that can reasonably be said to have a phylogenetic basis.

We here recognize three subfamilies – Sigmagraptinae n. subfam., Isograptinae Harris 1933, and Dichograptinae Lapworth 1873 – the phylogenetic rationale of which is discussed under the appropriate systematic headings below.

Subfamily **DICHOGRAPTINAE** Lapworth, 1873

DIAGNOSIS (provisional). Sicula generally relatively short, curved distally so that apertural region is commonly brought into phase with thecae of stipe^2; development generally isograptid but usually lacking isograptid symmetry; *artus* type development rare; dichotomies from one to many or lacking altogether.

DISCUSSION. We retain for the time being the Dichograptinae as a polyphyletic taxon including several genera (*Tetragraptus* and *Didymograptus, sensu lato*) which are still not definable in phylogenetic terms. For reasons stated above (p. 180) we do not accept the upgrading of these genera into higher taxa (e.g. Mu 1958, Mu *et al.* 1979) as this merely compounds the problems in defining natural groups. In the present work proximal end structure is regarded as important in the discrimination of taxa at subfamily level or above, and branching patterns alone – for example, the number of terminal stipes – are considered to be more subject to problems of parallelism.

Dichograptinae in the strict (phylogenetic) sense should be based on the proximal end structure of *Dichograptus* itself. The development of *D. octobrachiatus* was illustrated by Braithwaite (1976: pl. 10, figs 4–6). It is typified by a sicula about 1·5 mm in length. Theca 1^1 originates in the prosicula and grows considerably longer than the sicula; it diverges from the ventral side of the sicula, at the level of the sicular aperture, exposing about half the total length of its ventral wall. Theca 1^2 grows to similar proportions on the other side of the sicula; the two initial thecae thus form a symmetrical pair on either side of the sicula. Development is of isograptid type and dextral mode, as shown in Braithwaite's (1976) fig. 6B. Subsequent branching appears to be much like that of *T. serra* (p. 201) and *T. reclinatus* (p. 204) as described in this paper. The proximal region has a characteristic appearance with the small 'tooth' of the aligned distal part of the sicula midway between the apertures of $th1^1$ and $th1^2$. We can match this proximal type in several dichograptid species, as well as in the *T. serra* group of *Tetragraptus*. The structure is seen in *Didymograptus (Expansograptus), sensu stricto* (p. 231), and it would be surprising if it did not pertain in such genera as *Orthodichograptus* and *Schizograptus*. Together, these might form a phylogenetically-defined Dichograptinae. However, there are several problems which would make this premature. The type species of *Dichograptus* is the relatively slender species *D. sedgwickii,* the development of which is not described; we are uncertain of the relationship of the pendent and deflexed dichograptoids to this group; and there has to be a subfamily available to accommodate the many species with unknown development – dichograptids *sensu lato* – for which Dichograptinae is most appropriate.

For these reasons we adopt the concept of Dichograptinae *sensu lato* in this paper. Because of its polyphyletic nature, the above diagnosis is provisional. Although isograptid development greatly predominates throughout the group, isograptid symmetry is rarely achieved, providing a convenient means of distinguishing, for example, between reclined *Didymograptus* and the Isograptinae. In many didymograptids the sicula is curved so that the apertural region is deflected towards, and looks as if it is part of, $stipe^2$. However, the distal part of the sicula is commonly curved towards the $stipe^2$ side and its dorsal margin lies in contact with the ventral margin of $th1^2$; its apertural region is thus brought 'into phase' with thecal apertures of $stipe^2$. The effect is generally less marked, however, than in the Isograptinae where the sicula and $th1^1$ grow to identical proportions and the distal portion of the sicula forms an integral part of $stipe^2$.

Genus ***ORTHODICHOGRAPTUS*** Thomas, 1972

TYPE SPECIES. *Orthodichograptus robbinsi* Thomas 1972.

Orthodichograptus robbinsi Thomas 1972

Fig. 10

STRATIGRAPHIC RANGE. Lower Olenidsletta Member, 20 m from base on Olenidsletta, early Arenig (late Bendigonian), V_1b.

MATERIAL. PMO NF2052.

DISCUSSION. *Orthodichograptus robbinsi* has hitherto been recorded only from its type locality near Bendigo, Victoria, Australia. A second occurrence of the type and only species is therefore of some interest. It is found in Spitsbergen with a latest Bendigonian assemblage, as it is in Australia. As Thomas (1972) remarked, it is essentially like *Dichograptus octobrachiatus* in structure, but develops additional dichotomies distally. Our specimen with proximal end is like the type specimens in proportions, although the central disc is not preserved in the impure limestone Olenidsletta lithology. Several of the stipes show the fourth-order branches. Fragments of larger specimens are associated with that showing the proximal end, and attest to the very large size reached by this species.

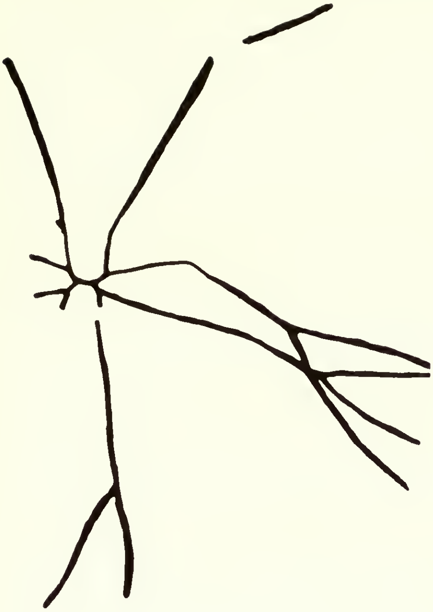


Fig. 10 *Orthodichograptus robbinsi* Thomas, PMO NF2052, 20 m above base of Olenidsletta Member on Olenidsletta; × 1.

Genus ***DICHOGRAPTUS*** Salter, 1863

TYPE SPECIES. *Dichograptus sedgwicki* Salter 1863.

Dichograptus maccoyi maccoyi Harris & Thomas 1940
Fig. 11

1940 *Dichograptus maccoyi* Harris & Thomas: 129; pl. 1, fig. 1a–d; pl. 2, fig. 2.
non 1979 *Dichograptus maccoyi* Harris & Thomas; Cooper: 58–59, fig. 25; pl. 5f.

STRATIGRAPHIC RANGE. Lower part of Olenidsletta Member, 22 m from base, at top of Bendigonian faunas (early Arenig).

MATERIAL. PMO NF2796.

DISCUSSION. Harris & Thomas (1940) originally described this species from the Bendigonian of Victoria. Cooper's (1979) material is from a much younger horizon, and we can also recognize a younger form in Spitsbergen, which we here regard as different enough from *D. maccoyi maccoyi* to be accorded subspecific recognition (below). All the figures of Harris & Thomas

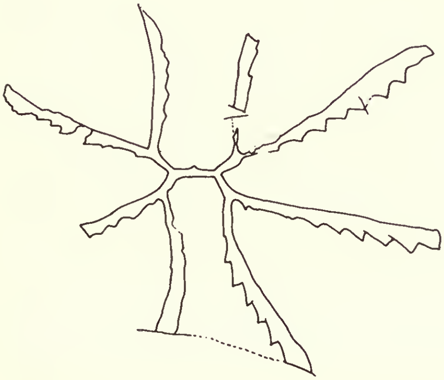


Fig. 11 *Dichograptus maccoyi maccoyi* Harris & Thomas, PMO NF2796, 20 m above base of Olenidsletta Member; × 3.

show narrow stipes, 1·4 mm wide at most, and generally about 1·5 cm long. There is little indication of more than the gentlest curvature of the stipes when flattened in profile, and the species must, at most, have been only gently reclined. Thecal apertures are 1 mm apart or slightly more, giving a spacing of 9–10 in 10 mm. The length of the first- and second-order stipes is also close to 1 mm, which indicates that the early dichotomies happened at successive thecae. Our specimen agrees exactly with the original description, except that the stipes do not exceed 1 cm in length, a difference we do not regard as important.

Dichograptus maccoyi densus subsp. nov.
Fig. 12

1979 *Dichograptus maccoyi* Harris & Thomas; Cooper: 58–59, fig. 25; pl. 5f.

DIAGNOSIS. A subspecies of *D. maccoyi* with distinctly reclined stipes less than 1 cm long; thecal spacing 13–14 in 10 mm.

STRATIGRAPHIC RANGE. Upper part of Olenidsletta Member, V_3b, late Arenig, Castlemainian (Ca_2) (= *Didymograptus hirundo* Zone).

MATERIAL. **Holotype,** PMO NF3223; paratypes many specimens on NF3218, NF3220; NF3219.

NAME. 'Densely spaced.'

DESCRIPTION. Our most complete rhabdosome, the holotype, is about 1·5 cm across; none of the individual stipes are longer than 6 mm. The eight stipes show distinctly curved dorsal walls when flattened in profile, and it is certain that the rhabdosome was reclined after the proximal four-stipe stage. One small growth stage shows the sicula, preserved somewhat oblique to the primary stipes, slender, about 1·3 mm long. Funicle 1·8–2·5 mm long, usually preserved dorsal side uppermost, with a diameter of 0·25–0·3 mm; one specimen shows a thecal aperture almost on a level with the first dichotomy. Second-order stipes 1 mm long or slightly less, and enclosing an angle of 100°–120°, again presenting their dorsal aspect. The third dichotomy includes an acute angle (as seen in the flattened state) and the stipes are presented in profile. They widen rapidly over three or four thecae from 0·5 mm to 1·2 mm, and appear to maintain constant width thereafter. Thecae are inclined at about 40°. They present different included angles between the free ventral wall and the apertural margin according to the angle of flattening, but in true profile this angle is about 80°. Thecae are densely spaced, the distance between apertures about 0·7 mm, corresponding to a thecal spacing of 13–14 in 10 mm.

DISCUSSION. This species agrees closely with *D. maccoyi maccoyi* in its proximal end structure, and it seems appropriate to accord the differences subspecific rank only. However, the strong curvature of the stipes, their rapid widening to 1·2 mm, and the dense thecal spacing (13–14 in 10 mm as compared with 9–10 in 10 mm) are distinctive enough to place our population outside the nominate subspecies. Cooper's (1979) specimen from New Zealand, although from a slightly

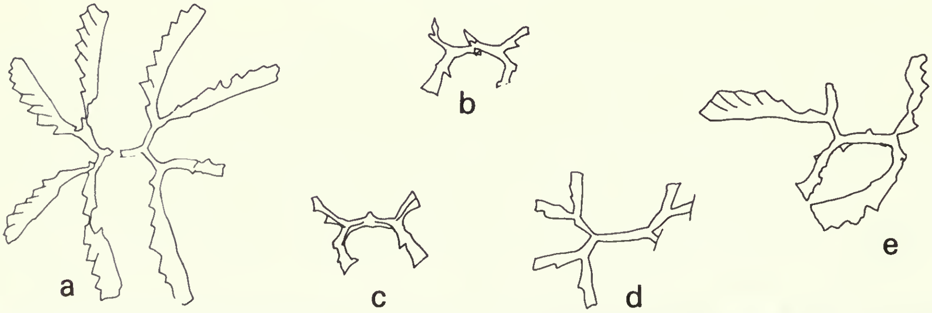


Fig. 12 *Dichograptus maccoyi densus* subsp. nov. a, PMO NF3223. **Holotype.** b, NF3218b. c, NF3220. d, NF3218a. e, NF3218. All from upper part of Olenidsletta member, 130 m above base; × 3.

higher horizon, is closer to *D. maccoyi densus* than to *D. maccoyi maccoyi* with regard to thecal spacing. Of other slender *Dichograptus* species, that named by Harris & Thomas (1940) as *D. norvegicus* has straight stipes, with long, narrow thecae 8 in 10 mm distally, while *D. changshanensis* Mu 1957 has much more slender stipes, only 0·55 mm wide distally. There may prove to be a complete transition stratigraphically between *D. maccoyi maccoyi* and *D. maccoyi densus*. We have one small growth stage (NF1719) which may belong here, and which occurs midway between the two subspecies stratigraphically.

Dichograptus solidus Harris & Thomas 1940

Fig. 13

1940 *Dichograptus octonarius* var. *solida* Harris & Thomas: 129–130; pl. 1, fig. 3; pl. 2, fig. 4.
1979 *Dichograptus octonarius* J. Hall; Cooper: 59; pl. 5e; fig. 26.

STRATIGRAPHIC RANGE. Olenidsletta Member, V_1b and V_3, 21–116 m above base. Bendigonian to Castlemainian.

MATERIAL. PMO NF3359, NF3360.

REMARKS. The rhabdosome is formed by progressive branching to three orders of apparently consecutive dichotomy. Details of sicula and proximal structure unknown. First-order stipes are together 2 mm long, second-order stipes are about 1 mm long. Third-order stipes are about 20 mm long; they are curved, concave dorsally and are inclined to the bedding plane by rotation along their sagittal axis. Their original attitude in the rhabdosome appears to have been weakly to strongly reclined. Third-order stipes widen rapidly, reaching a maximum of at least 3 mm. Thecae are spaced about 9 in 10 mm.

The Spitsbergen specimens most closely match the reclined forms of *Dichograptus* from the Castlemainian and Yapeenian of Victoria figured by Harris & Thomas (1940: pl. 1, figs 2a–b) as *Dichograptus octonarius* Hall and *D. octonarius* var. *solida* Harris & Thomas. The specimen NF3359, with strongly reclined stipes, resembles that figured by Cooper (1979: fig. 26) from the Castlemainian of New Zealand and referred to *D. octonarius*. A reclined rhabdosome seems to have become regarded as characteristic of *D. octonarius*. Yet a reclined attitude of stipes was not mentioned by Hall and is not determinable in his single figured specimen from Levis; a 'pseudo-reclined' appearance in this specimen results from some stipes being folded over on themselves.

It therefore seems unwise to continue using Hall's name. The next available name for the reclined forms appears to be *Dichograptus solidus* Harris & Thomas 1940.

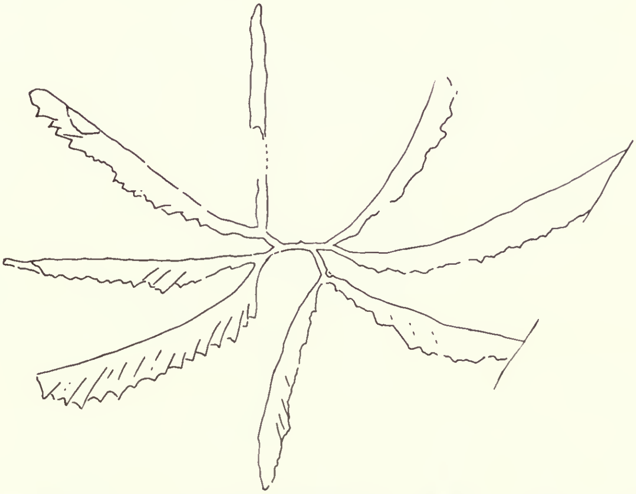


Fig. 13 *Dichograptus solidus* Harris & Thomas, PMO NF3360, 21–22 m above base of Olenidsletta Member; × 2.

Third-order stipes in our specimens are slightly less broad than in those of the holotype figured by Harris & Thomas, a difference that may be partly or wholly accounted for by the fact that our stipes are twisted and do not present the full dorsoventral profile.

Dichograptus octobrachiatus Hall 1858
Pl. 2, fig. 3

Stratigraphic range. Through most of the Olenidsletta Member, 10–105 m from base, spanning most of the Arenig (Bendigonian to Castlemainian), and V_1a–V_3. Abundant only in the late Bendigonian part of the section.

Material. Includes PMO NF828, NF4171, SM A105817–8 and many others.

Discussion. Material from Spitsbergen is flattened, and adds little to previous information about this widespread species. Proximal end development appears to have been like that of *Tetragraptus serra,* described in detail here (p. 195), and the mature rhabdosome results from progressive branching, by consecutive dichotomies, to the third order. The last dichotomy of some second-order stipes is suppressed resulting in six- or seven-branched rhabdosomes, which are not uncommon in our late Bendigonian assemblages. Distal stipes are straight, which is the main difference from *D. solidus.* Length of 'funicle' is 2 mm, and secondary stipes 1·0–1·5 mm. Distal stipes reach 4·5 mm in width (including projecting flattened thecal apertures 0·5 mm long), but stipe width on most specimens is 3–3·5 mm. Thecal spacing is 10–11 in 10 mm on mature stipes. Curved thecal form appears to be identical to that of *Tetragraptus serra.*

Genus ***TETRAGRAPTUS*** Salter, 1863

Type species. *Fucoides serra* Brongniart 1828.

Classification of *'Tetragraptus'.* Quadriramous dichograptoids have traditionally been placed in Salter's genus *Tetragraptus.* It has long been recognized (Nicholson & Marr 1895, Elles 1922) that such a diverse range of forms was bound to include members of different phyletic lineages. The above authors and Bulman (1955, 1963, 1970) regarded *Tetragraptus* as representing a stage or grade in the transition from multiramous to pauciramous species along a number of different lineages. They thus accepted the form genus *Tetragraptus* as a polyphyletic, but useful, grouping of species.

Attempts to subdivide the genus (Bouček & Přibyl 1951, Bouček 1973, Obut 1957, Ruedemann 1904) have generally followed the same lines as those of attempts to subdivide *Didymograptus* and they suffer from the same shortcomings. Many of our comments in discussion of the classification of *Didymograptus* apply here, particularly those relating to the use of general rhabdosome shape as the principal basis of generic classification. Features of general rhabdosome morphology, particularly the attitude or arrangement of second-order stipes, have been used as either the sole, or the main, basis for recognizing subgenera or genera within the old concept of *Tetragraptus.* The following have been proposed: *Tetragraptus (Etagraptus)* Ruedemann 1904, *T. (Eotetragraptus)* Bouček & Přibyl 1951, *Pendeograptus* Bouček & Přibyl 1951, *Paratetragraptus* Obut 1957, *Tetragraptus, s.s.* or *Tetragraptus (Tetragraptus)* Bouček & Přibyl 1951. The second, third and fifth of these were, in effect, merely formal upgradings of the three informal groups of tetragrapid species of Elles & Wood 1902. All five were regarded as synonyms by Bulman (1970) who maintained the broad concept of *Tetragraptus* as a form genus, but the subgenera were raised to full generic rank by Bouček (1973) who reaffirmed his faith in their phyletic integrity.

1. Subgenus *Etagraptus* Ruedemann, 1904, was based on *T. (E.) lentus* Ruedemann 1904. It was extended to include those tetragraptids with H-shaped rhabdosomes such as the important zonal species *T. approximatus.* However the type, *T. (E.) lentus,* is a distinctive form with long slender sicula and initial pair of thecae, characters which distinguish it from *T. approximatus* and its allies, but which link it with species here assigned to the Sigmagraptinae. Thecae of

second-order stipes match those of sigmagraptines and differ markedly from those of the *T. approximatus* group. *Etagraptus* is therefore here regarded as belonging to the Subfamily Sigmagraptinae and is further discussed under that heading. For the remaining species included by Ruedemann in *Etagraptus,* the name *Paratetragraptus* Obut 1957 is used.

2. Subgenus *Eotetragraptus* Bouček & Přibyl, 1951, was erected to include species with stipes developed in the horizontal plane. It originally included those with H-shaped rhabdosomes but was later (Bouček 1973) restricted to species in which the second-order stipes are disposed more or less at right angles. *T. quadribrachiatus* is the type species. However, according to its definition, the subgenus also includes such improbable companions as *T. headi,* with its long curved thecae of *T. serra* type, and *T. harti,* with slender thecae of low inclination. It seems highly improbable that these three forms are closely related. Unfortunately the development and proximal structure of *T. quadribrachiatus* are not known as the species has not yet been described from relief material. It is thus not possible to define the subgenus *Eotetragraptus* in a phyletically meaningful way and it is not used here.

3. The genus *Pendeograptus* Bouček & Přibyl, 1951, was erected for tetragraptids with pendent rhabdosomes and was based on *T. pendens* Elles 1898. It includes *T. fruticosus* and a number of forms close to *T. fruticosus* or *T. pendens* figured by Ruedemann (1947: pl. 51); also such forms as *T.* cf. *pendens* of Cooper (1979: fig. 34a; pl. 6c). Some details of the proximal region of *T. fruticosus (s.l.)* are known from material we describe herein. The sicula is long and wedge-shaped, and $th1^1$ relatively straight; the whole aspect of the proximal region resembles that of a bryograptid rather than of a dichograptid. Development is of isograptid type. Thecae of second-order stipes have acute, projecting, denticulate apertural margins and deeply recessed apertural 'excavations', again more like thecae of a dendroid than of a graptoloid. Once again, however, details of the proximal region of the type species, *T. pendens,* are unknown and the species has not yet been described from relief material. For this reason, inclusion of *T. fruticosus* within the genus, and the validity of the genus itself, is provisional. Specimens figured as *T. pendens* from Victoria by Thomas (1960: pl. 3, fig. 31), from New Zealand by Cooper (1979: fig. 34a; pl. 6c) and from North America by Ruedemann (1947: pl. 51, figs 18–25) suggest that there is an array of forms lying between *T. fruticosus* and the typical *T. pendens* of Elles, supporting the inclusion of both within the one genus. We therefore tentatively accept *Pendeograptus* as a subgenus of *Tetragraptus,* redefined on proximal characters.

4. The genus *Paratetragraptus* Obut, 1957, was erected for *T. approximatus* and its allies with H-shaped rhabdosomes, but excluding *T. lentus* Ruedemann, 1904, which is not closely related to *T. approximatus.* The group so defined would include *T. acclinans* Keble, *T. vestrogothus* Törnquist and the various forms from North America figured by Ruedemann (1947: pl. 52, figs 4–27), and does appear to be reasonably distinct and definable on its rhabdosome shape. Included forms are all of similar age (basal Arenig), have generally similar thecal characteristics, and might well constitute a monophyletic group.

Sicular morphology and proximal structure are not known in *T. approximatus,* or for that matter in any other member of the group, and its recognition as a valid subgenus remains unsupported by data on proximal morphology. Our acceptance of *Paratetragraptus* as a subgenus is therefore provisional. In life, the stipes presumably lay in a horizontal plane with respect to the sicula, since the sicula is almost invariably not seen in profile view.

5. *Tetragraptus, sensu stricto* as used by Bouček (1973) includes groups IV *(T. serra)* and V *(T. bigsbyi)* of Elles & Wood 1902. Bouček's diagnosis is as follows:

'Rhabdosome pendent [sic], sicula well developed, free. Stipes more or less parallel to sicula; at least one stipe of each pair of stipes in a reclined up to scandent position. When preserved in horizontal plane, thecae of one pair of stipes are on the inner side, those of the other pair on the external side of the stipes'. Type species is *Fucoides serra* Brongniart 1828. From the diagnosis the group is defined principally on the possession of strongly reclined (assuming that the word 'pendent' in the diagnosis is a misprint) or scandent stipes. From his list of included species (Bouček 1973: 20 – *T. amii* Elles & Wood, *T. bigsbyi* (Hall), *T. erectus* Mu, Ge & Yin, *T. kindlei* Ruedemann, *T. phyllograptoides* Linnarsson, *T. pseudobigsbyi* Skevington, *T. taraxacum* Ruedemann and *T. woodae* Ruedemann) all degrees of reclination, from weakly reclined *(T. amii)* to highly inclined *(T. bigsbyi)*, are included, although the former would appear to be excluded by the diagnosis.

The group contains the type species of the genus *Tetragraptus* Salter, 1863, *T. serra,* some proximal details of which are interpreted herein from isolated growth stages from Spitsbergen. The sicula is very long and massive, the first theca arising near the apex of the sicula on its ventral (virgellar) side. The growth and development, as far as can be traced, is similar to that in the better known *T. bigsbyi* (Bulman 1970: fig. 53), *T. reclinatus reclinatus, T.r. toernquisti* and *T. phyllograptoides,* the last three of which are described herein. The differences between them are slight to moderate differences of size and tenuity of the sicula and proximal thecae and we would not rank them as important differences in structure.

There is thus a group of species with proximal features similar to those of *T. serra* and, by definition, this group should be regarded as *Tetragraptus, s.s.* The concept of *Tetragraptus, s.s.*, as the nominate subgenus, is thus retained but is here based on proximal features as well as, rather than solely on, stipe attitude.

For the majority of species at present referred to the form-genus *Tetragraptus,* and in which proximal morphology is unknown, the general (form-genus) concept of *Tetragraptus* must be retained. As with the didymograptids it may be some time before we can switch over to a wholly phylogenetically based classification. The form-genus *Tetragraptus, s.l.,* is here used to include the majority of (poorly known) species together with the three phyletically-based subgenera. We stress that we do not imply the subgenera are phyletically related within the old form-genus. It is much more likely that *Pendeograptus* and *Paratetragraptus* are more closely related to species and genera outside *Tetragraptus, s.l.,* than to those within it, and that they will eventually be raised to full generic rank. The system has the advantage of retaining a measure of nomenclatorial stability, especially for important zonal species such as *T. (Paratetragraptus) approximatus* and *T. (Pendeograptus) fruticosus* while yet using a grouping that reflects inferred phyletic relationships. It should be recognized that, as with *Didymograptus,* the proposed classification is in concept a dual one.

Form-genus ***TETRAGRAPTUS*** Salter, 1863 *(= Tetragraptus, s.l.)*

Subgenus ***TETRAGRAPTUS*** Salter, 1863

TYPE SPECIES. *Fucoides serra* Brongniart 1828.

DIAGNOSIS. Sicula long and broad, th1^1 arising near apex and diverging sharply from near base. Thecae 1^2 and 2^1 grow out horizontally, their proximal portions together forming a massive structure representing the two 'crossing canals'. Development of isograptid type, dextral or, rarely, sinistral. Dicalycal th3^1 (right-handed) and th3^2 (left-handed), all development on the reverse side. Two orders of progressive dichotomy. Second-order stipes reclined to scandent, thecae curved with high distal inclination.

SPECIES: *Fucoides serra* Brongniart 1828, *Graptolithus bigsbyi* Hall 1865, *Tetragraptus phyllograptoides phyllograptoides* Strandmark 1902, *T. p. triumphans* Cooper & Fortey subsp. nov., *T. reclinatus reclinatus* Elles & Wood 1902, and *T. r. toernquisti* Monsen 1937.

The following species are provisionally included: *Tetragraptus amii* Elles & Wood 1902, *T. bigsbyi* var. *divergens* Monsen 1937, var. *askerensis* Monsen 1937, and var. *ascendens* Monsen 1937, *T. reclinatus abbreviatus* Bouček 1956, *T. pseudobigsbyi* Skevington 1965, *T. rigidus* Ge 1964, *T. hsui* Ge 1964, and *T. isograptoides* Ge 1964.

The following are doubtfully included: *Tetragraptus mobergi* Monsen 1937, *T. woodae* Ruedemann 1904, *T. minutus* Ge 1964, and *T. ovalis* Ge 1964.

DISCUSSION. The proximal morphology and development are known in detail in several species. The sicula is relatively massive and the first theca diverges from it at a sharp angle. Thecae 1^2 and 2^1 diverge from each other in the horizontal plane and their proximal portions together form a massive bulge on the reverse side of the sicula and th1^1. The initial portion of th1^2 is dorsoventrally wide, equivalent to about ⅓ the length of the sicula. The second-order stipes are produced from dicalycal thecae 3^1 (which is right-handed) and 3^2 (left-handed), the branching type on both sides being isograptid. All development thus takes place on the reverse side of the rhabdosome. The reclined growth of second-order stipes commences from their first theca in *T. (T.) serra* and *T. (T.) phyllograptoides triumphans,* but is more gradually introduced in *T. (T.) reclinatus reclinatus* and *T. (T.) r. toernquisti.*

The species provisionally included above are known only from flattened material. Details of their proximal morphology are not known but they have a general resemblance in rhabdosome form. Those doubtfully included are too poorly known or described to allow a reasonably confident assignment. It is highly probable that several of the above-listed names are synonyms.

Tetragraptus (Tetragraptus) serra serra (Brongniart 1828)

Figs 14a–e, 15a–e, 16, 17, 18; Pl. 3, fig. 5

1828 *Fucoides serra* Brongniart: 71; pl. VI, figs 7, 8.
1858 *Graptolithus bryonoides* J. Hall: 126.
1865 *Graptolithus bryonoides* J. Hall; Hall *(pars)*: 84; pl. III, figs ?11, ?12; pl. IV, figs 1, 4, 6–8, ?11; *non* pl. IV, figs 9, 10 (= *T. amii* Elles & Wood); *non* pl. IV, figs 2, 3 (= *T. reclinatus toernquisti* Monsen).
1875 *Tetragraptus bryonoides* (Hall) Nicholson: pl. VII, figs 4, 5.
1877 *Graptolites (Didymograpsus) bryonoides* (Hall) M'Coy: 16–17; pl. 2, figs 2, 3, ?5.
1902 *Tetragraptus serra* (Brongniart) Elles & Wood *(pars)*: 65–67; pl. VI, figs 4a–c, f only.
1904 *Tetragraptus serra* (Brongniart); Ruedemann *(pars)*: 655–657, text-figs 56, 57; pl. 11, figs 8–10 only.
1904 *Tetragraptus serra* (Brongniart); Törnquist: 8–10; pl. 1, figs 17–21.
1937 *Tetragraptus serra* (Brongniart); Monsen: 169; pl. 4, figs 13, 18, ?22, ?28; pl. 12, figs 2, 3; pl. 19, fig. 10.
1960 *Tetragraptus serra* (Brongniart); Thomas: figs 28–30.
1960 *Tetragraptus serra* (Brongniart); Berry: 56; pl. 6, fig. 6; pl. 13, fig. 1.
1963 *Tetragraptus serra* (Brongniart); Ross & Berry: 79–80; pl. 3, fig. 6.
1979 *Tetragraptus serra* (Brongniart); Cooper: 66; pl. 8i; fig. 36a.

Type material

Lectotype. BM(NH) 26995, herein selected; paralectotypes, BM(NH) Q5060–2. All specimens lie in the one bedding plane on a small slab of dark grey shale, and are housed in the British Museum (Natural History). There are no other recognizable species in the slab.

The original specimens of Brongniart's *Fucoides serra,* like those of his *Fucoides dentatus* (Bulman 1963), have long been believed lost and the identity of the form *serra* has been the subject of much confusion, particularly in relation to *Tetragraptus amii* Elles & Wood and *Graptolithus* [*Tetragraptus*] *bryonoides* J. Hall.

The original slab was collected from Point Levis by 'M. Stockes' (probably Charles Stokes), and acquired by Dr Bigsby who eventually presented it to the British Museum as part of a larger collection of Levis material; it has remained unrecognized as such until the present. From Brongniart's somewhat diagrammatic figures, particularly that showing the whole slab with five fragmentary rhabdosomes (1828: pl. VI, fig. 7), there can be no doubt that slab now in the BM(NH) is that used by Brongniart in erecting the species. The uppermost rhabdosome in his fig. 7 is that refigured here as Fig. 14e and the lower group of rhabdosomes are refigured here in Fig. 14a–d. The specimen of Fig. 14e, which is here chosen as **lectotype**, is the most complete and also most clearly shows the reclined attitude of the stipes.

Stratigraphic horizon. The horizon from which the lectotype comes is, unfortunately, unknown. '*T. serra*' is listed from Zones A, C1, D1 and D2 by Raymond (1914).

Description of type series. Details of sicula and proximal development and structure are not visible. Primary stipes apparently composed of one theca each. Second-order stipes up to 24 mm long, moderately reclined, with gentle, dorsally concave curvature following their

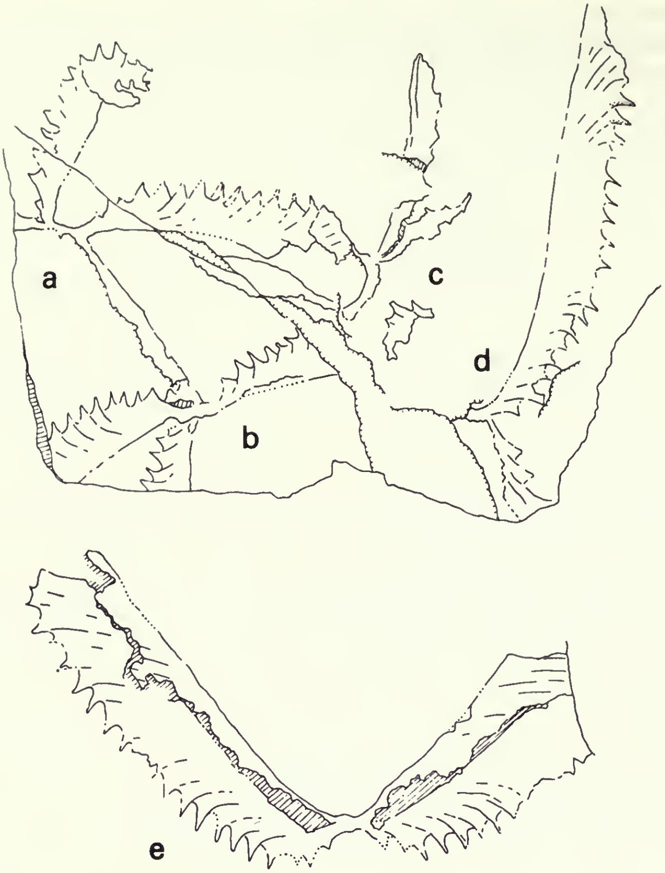


Fig. 14 *Tetragraptus (Tetragraptus) serra serra* (Brongniart), type specimens. a–d, paratypes, preserved near edge of slab, the outline of which is shown: a, BM(NH) Q5060; b, Q5061; c, fragmentary specimen; d, Q5062. e, **lectotype,** BM(NH) 26995, in same slab as paratypes. All × 2·5.

initial sharper curvature, becoming straight distally. Stipe width at the level of any given thecal aperture varies from specimen to specimen (Fig. 15); maximum stipe width ranges from about 3·7 mm (Q5062) to 4·2 mm in the lectotype (26995). Some of this variation is probably the result of the preservation process (see below) but some is likely to reflect variation in the original rhabdosomes. It is not possible to determine the relative proportions of each except to note that in Q5062, with relatively narrow stipes, the apertural margins show deep 'excavations' and thecal inclination is not noticeably reduced. This suggests that the stipe was orientated with its sagittal plane more or less parallel with the plane of bedding prior to burial and not rotated to present a partially dorsal view. Thus its narrow stipes are a primary feature and the range of the population in original dorsoventral stipe width is likely to have been considerable.

Thecae are strongly curved, particularly near their apertures where their angle of inclination exceeds 90°. Ventral apertural margins project prominently and lateral apertural margins are deeply recessed, producing deep 'excavations'. They are spaced 8·5 in 10 mm in the lectotype, and 8·6 to 9·5 in 10 mm in the paralectotypes.

DISCUSSION of type series. The lectotype and paralectotypes together show well the variation that can be introduced by distortion of the rhabdosome prior to and during burial. Because of the attitude of its stipes it is inevitable that, when the rhabdosome is preserved in a flat plane, as

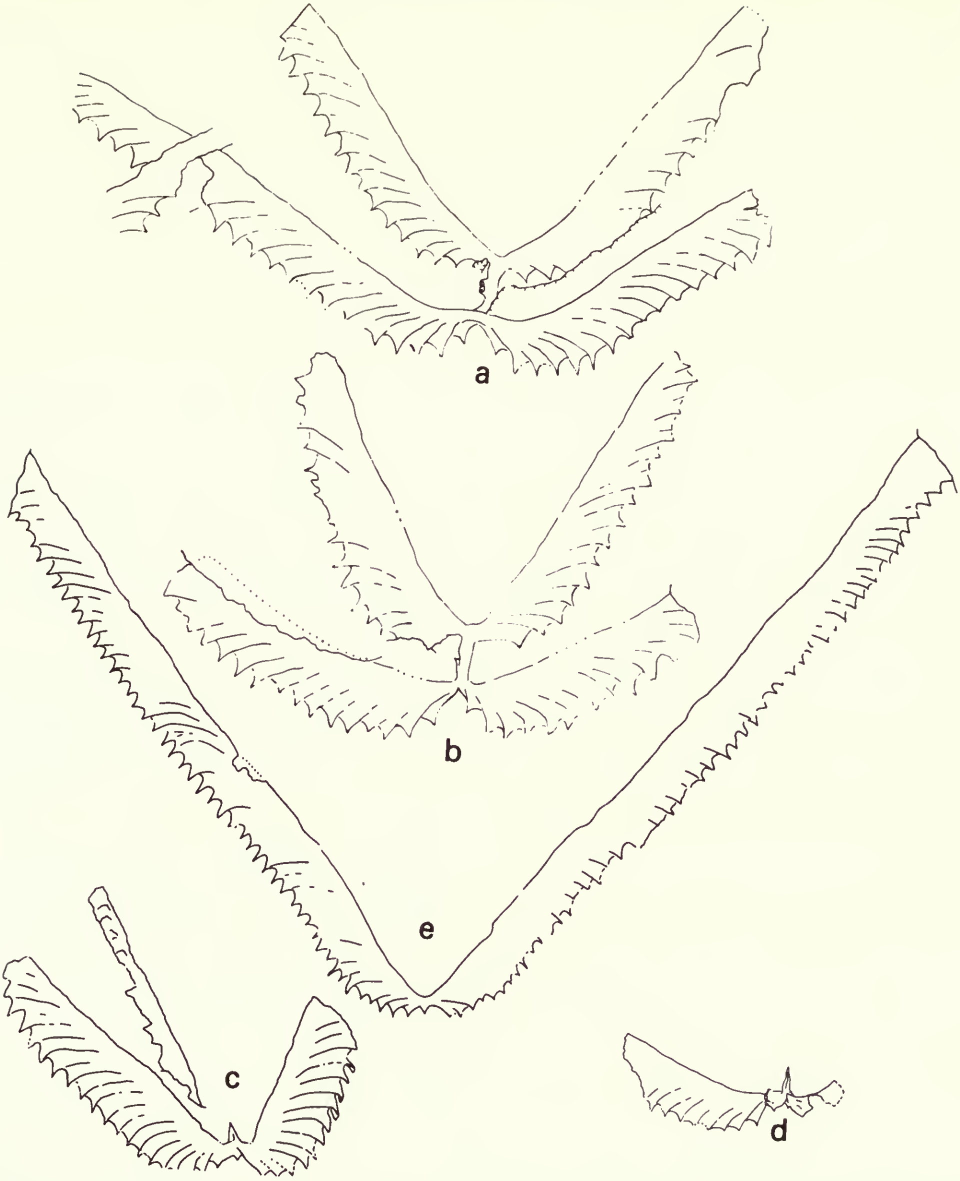


Fig. 15a–d *Tetragraptus (Tetragraptus) serra serra* (Brongniart) from Spitsbergen. a, SM A105789, mature rhabdosome preserved in relief in limestone, 15–24 m above base of Olenidsletta Member, southern section; × 3. b, A105743, lower part of Olenidsletta Member on Olenidsletta (see Pl. 3, fig. 5); × 3. c, PMO NF2788, 23 m above base of Olenidsletta Member, southern section; × 2·5; d, A105792, in partial relief, 15–24 m above base of Olenidsletta Member, × 2·5.

Fig. 15e *Tetragraptus (Tetragraptus) serra* subsp. 1. A105801, 9·5–15 m above base of Olenidsletta Member, southern section; × 1·7.

is usual in shale, it will suffer distortion and rotation of the stipes. If it is preserved 'on its side', with either the median plane or bilateral plane of the rhabdosome parallel to the bedding, the upper pair of stipes fold down upon the lower pair of stipes, both pairs retaining their reclined attitude, as in Fig. 14e. On the other hand, if it is preserved on its base (or inverted, on the tips of its stipes) then the stipes will be splayed out and one or more will usually be bent or rotated.

There are all intermediates between the two end modes, and a great range in the final attitude of the stipes results. Also, measurements of stipe width are likely to be decreased by torsion along the stipe or twisting, so that it is not seen in full profile view, particularly in rhabdosomes preserved in the second mode above.

These factors undoubtedly contribute to the variation shown by the type series, and in populations from Spitsbergen and elsewhere. There is little doubt that the lectotype and paralectotypes all represent the one species, despite their wide range of variation in stipe attitude and width. Some of the variation no doubt reflects morphological variation of the original rhabdosomes but some, particularly that in stipe attitude, results from the vagaries of preservation. For these reasons there seems little point in attempting to distinguish species in flattened material on subtle differences in stipe attitude and width.

RELATIONSHIPS with *Graptolithus bryonoides* J. Hall and *Tetragraptus amii* Elles & Wood. The name *Graptolithus bryonoides* was introduced by Hall in 1858 but was accompanied neither by figures nor by specification of specimens studied by him. His fuller description and figures of 1865 can be regarded as a subsequent validation and the figured specimens as syntypes. Nine specimens were figured, of which two (those of his pl. 3, figs 11, 12, and pl. 4, fig. 4) were only questionably included in the species. In a footnote Hall (1865: 84) states 'I have little doubt that this species is identical with *Fucoides serra* of Brongniart . . .', of which he had only recently become aware, and 'the figures of Brongniart correspond with figs 9 and 10 of plate 4 of this memoir'. Although in the figure caption of these two specimens Hall had added the proviso that 'Figs 9 and 10 may possibly prove to be a distinct species' he nevertheless clearly regarded the name *bryonoides* as being a junior synonym of *Fucoides serra*.

Most subsequent authors, however, have considered Hall's *bryonoides* to comprise two forms, one 'in which the stipes are spread out in what may be termed a *"quadribrachiatus"* fashion' (i.e. more or less horizontal), represented by his figs 9 and 10, and one 'in which the stipes are directed obliquely upward' (reclined) represented by pl. 4, figs 1–8, 11 (Elles & Wood 1902: 66). Opinions as to which of the two forms the name *serra* should apply have differed, unfortunately, leading to much confusion in meaning of the name *serra*. Whereas Elles & Wood regarded the reclined form as *serra* and the 'horizontal' form as identical with Lapworth's (MS) species *Tetragraptus amii*, Törnquist (1904) took the opposite view and regarded the 'horizontal' form as *serra* and, although he did not state so specifically, the reclined form as *bryonoides*. Some subsequent Swedish and most Australasian workers have followed Törnquist, using the names *serra* and *bryonoides* whereas most British and North American workers have followed Elles & Wood and used the names *amii* and *serra* respectively for the same two species. The latter usage has clearly gained the widest acceptance.

The problem can only be resolved by the designation of lectotypes and redefinition of the species. Rediscovery of the type specimens of Brongniart's *Fucoides serra* in the British Museum (Natural History) now enables us to do this and lectotypes for all three species are therefore proposed herein. It is necessary, however, to introduce a further complication. Among the specimens generally attributed to *T. serra, sensu* Elles & Wood, are two (Hall's 1865: pl. 4, figs 2, 3) which differ in having stipes which are narrow and declined rather than reclined and thecae with a lower angle of inclination. It would seem that the two specimens are unlikely to represent the same species as that represented by the others and they are here excluded and referred to *T. reclinatus toernquisti* Monsen.

LECTOTYPE for *Graptolithus bryonoides* Hall 1858. Various courses are open in the selection of a lectotype for *G. bryonoides*. The one which seems to be consistent with the most widely accepted usage is to select a specimen from the group referred to *serra* by Elles & Wood (excluding the specimens of pl. 4, figs 2 and 3), thus making *bryonoides* a junior synonym of *serra,* and to retain *amii,* based on British material, as a distinct species. Specimen GSC 978, held in the Geological Survey of Canada, Ottawa, and figured by Hall (1865) as pl. 4, figs 1 and 6, is therefore here designated **lectotype** and refigured (Fig. 16). Paralectotypes: GSC 922b, figured by Hall (1865: pl. 4, fig. 4); GSC 922a (Hall 1865: pl. 4, figs 7, 8); ?GSC 922g (Hall 1865: pl. 6, fig. 4), very poorly preserved. The originals of Hall's 1865: pl. 3, figs 11, 12, are

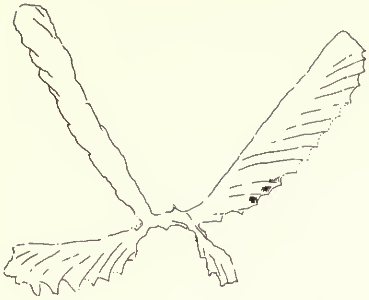


Fig. 16 *Tetragraptus (Tetragraptus) serra serra* (Brongniart). **Lectotype** of *Graptolithus bryonoides* Hall, GSC 978. Specimen figured by Hall (1865: pl. 4, figs 1, 6). × 2·5.

indeterminate stipe fragments and those of his pl. 4, figs 5, 11, although not seen by us, appear to be similarly incomplete and indeterminate. The originals of Hall's 1865: pl. 4, figs 9, 10 (not seen by us) are regarded as belonging to *Tetragraptus amii* Elles & Wood, and those of his pl. 4, figs 2, 3 as belonging to *Tetragraptus reclinatus toernquisti* Monsen.

Thus defined, *G. bryonoides* clearly belongs to Brongniart's species *Fucoides serra.* Stipe attitude, curvature and width, thecal spacing and outline match well. Maximum stipe length is 42 mm, longer than that of the types but unlikely to be of diagnostic value.

Ge (1964) separated the specimens of Hall's pl. 4, figs 4, 7, 8 and 11 and referred them to his new species *T. rigidus,* but there seems little justification in discriminating between these and that of Hall's fig. 2; they merely represent more advanced growth stages. *T. rigidus* from the Ningkuo Shales of late Arenig to Llanvirn age is distinguished from *bryonoides* (and *serra*) by its more robust rhabdosome and rigid, highly reclined stipes. It is probably the best name for the forms listed as *T.* cf. *serra* from the late Castlemainian and Yapeenian of New Zealand by Cooper (1979: 67; pl. 8, figs g, k).

Spitsbergen material

Stratigraphic range. Olenidsletta Member, V_1b, 9–25 m above base; early Arenig.

Material. SM A105789–93, PMO NF2787–8.

Description. Sicula 2·3 mm long (measured in specimen SM A105792). The first-order stipes are comprised of a single theca each. Second-order stipes increase rapidly in width, reaching a maximum of 3·0–4·0 mm by the level of the 5th to 8th theca (Fig. 17). Stipes are moderately reclined and initially curved but become straight distally, as in the type material. Maximum length 30 mm, but longer isolated stipe fragments may belong to the species.

Thecae in the mature part of the stipe are inclined initially at about 30°–35°; distally they are inclined to about 95° but the free ventral wall often appears to be flexed downwards apparently from deformation during burial (Fig. 15). Apertural margins are deeply recessed leaving a protruding ventral process, but again the outline of the apertural margin varies widely with mode of preservation. Thecae are spaced 9·5–11·5 in 10 mm in the proximal part of the stipe, and 9·0–10·0 in 10 mm in the distal part.

Development. Several growth stages have been isolated by acid treatment, of which two are figured (Fig. 18a, b). Although most have been flattened or otherwise distorted, they enable several details of development to be determined. Theca 1^1 originates high on the sicula, probably on the prosicula although this structure is not clearly defined. Theca 1^1 grows down the ventral side of the sicula and turns sharply out near the sicular aperture, as in *T. bigsbyi* (Bulman 1970: fig. 53). Theca 1^2 originates from 1^1 at a point level with the mid-length of the sicula. It immediately expands and gives rise to th2^1. The proximal portion of the th1^2 and 2^1 together comprise a massive structure, containing the 'crossing canals', on the reverse side of the rhabdosome. The whole aspect of the proximal region is more robust than in *T. bigsbyi.* Development is isograptid and dextral and conforms closely to that of *T. bigsbyi.* Details of second-order branching are unknown.

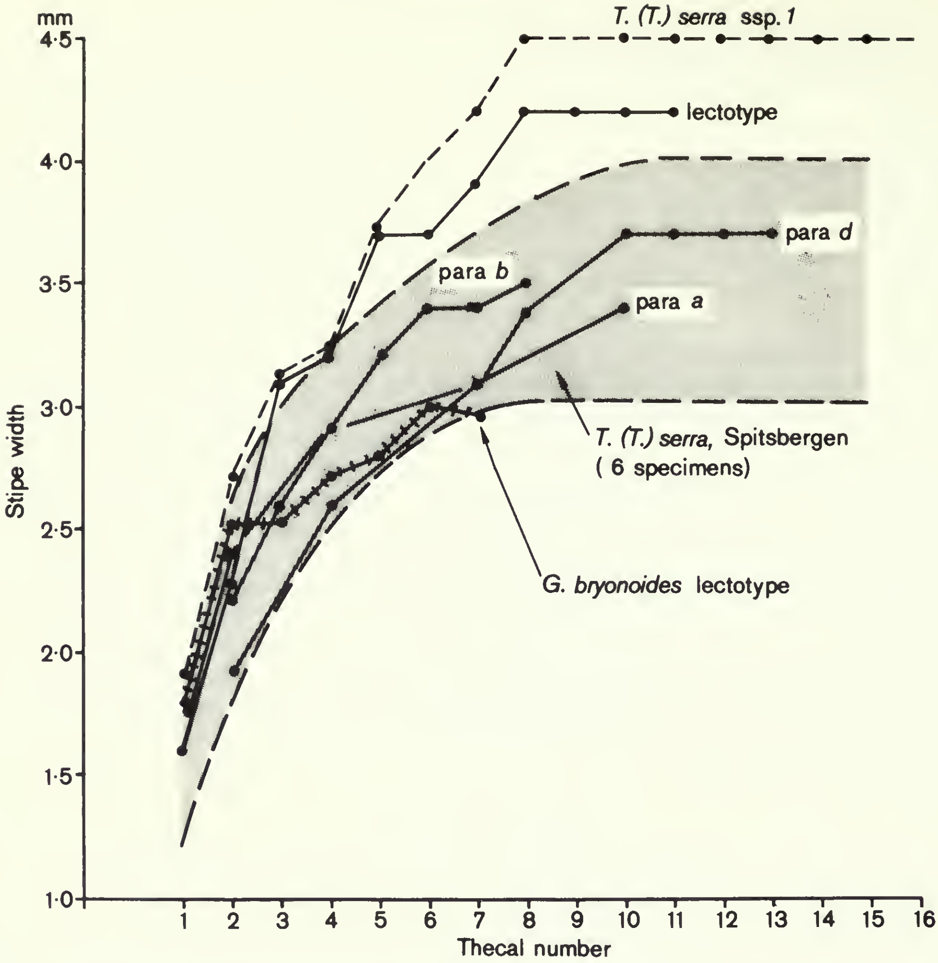


Fig. 17 Stipe expansion diagram, *Tetragraptus (Tetragraptus) serra serra* (Brongniart), type series, and the lectotype of *Graptolithus bryonoides* Hall (= *T. (T.) serra serra*). The field for 6 specimens from Spitsbergen is stippled. Expansion curve for *T. (T.) serra* subsp. 1 is also shown.

Discussion. The proximal structure of *T. serra*, as described here, not unexpectedly matches closely that of *T. bigsbyi* described by Bulman (1970: fig. 53). It differs from those growth stages assigned to *T.* cf. *serra* by Skevington (1965: figs 11–13) in the lower point of origin of th1^2.

The Spitsbergen material indicates a considerable range of variation in maximum stipe width, no doubt in part the result of preservation. It differs from the type material only in having fractionally narrower thecal spacing.

The comparatively wide range of stipe width here described for *T. serra* calls into question the distinctness of such species as *T. pseudobigsbyi* Skevington 1965 which are of *serra* type and whose maximum stipe width (2·9–3·2 mm) lies within the *serra* range. Several somewhat slender but poorly preserved forms are present in the Spitsbergen populations of *T. serra*. However, because of its closer thecal spacing (12–13 in 10 mm) *T. pseudobigsbyi* is retained as a distinct species. It should be noted that Skevington's figured specimens of both *T. pseudobigsbyi* and *T. bigsbyi* present an a, b stipe pair, rather than the more familiar orientation of a 1, 2 stipe pair with the sicula between them.

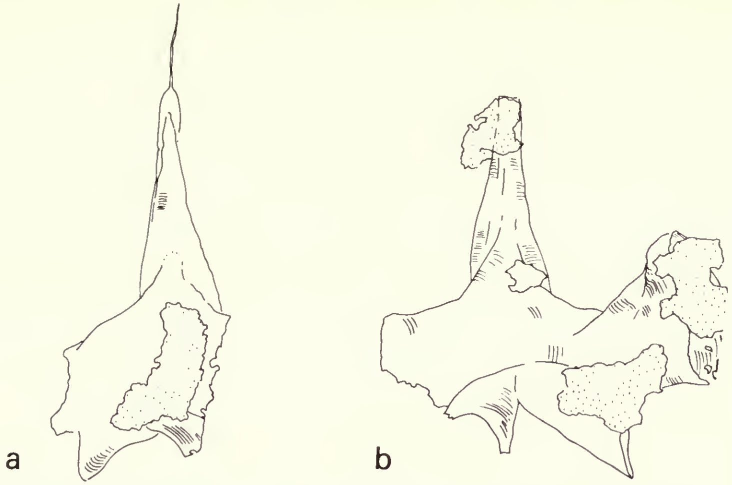


Fig. 18 *Tetragraptus (Tetragraptus) serra serra* (Brongniart), growth stages. a, SM A105795, fragmentary stage showing high origin of th1[1] and proximal portions of th1[2] and th2[1]. b, A105796, incomplete later stage showing apertural region of th1[1], proximal part of th2[1] and partly formed th3[1]. Both from 16–17 m above base of Olenidsletta Member, × 20.

None of the specimens figured by Ruedemann (1947: pl. 50, figs 19–23) under the name *T. serra* appear to belong to Brongniart's species, but two (those of his figs 22, 23) are referred to *T. serra* subsp. 1 below.

T. rigidus Ge (1964) from the Ningkuo Shale of China differs from *T. serra* only in its more rigidly reclined stipes and slightly more widely spaced thecae and is probably best regarded as a stratigraphically younger subspecies.

Tetragraptus serra subsp. 1

Fig. 15e; Pl. 5, fig. 8

1902 *Tetragraptus serra* (Brongniart) Elles & Wood *(pars)*: pl. 6, fig. 4d only.
1947 *Tetragraptus serra* (Brongniart); Ruedemann *(pars)*: pl. 50, figs 22, 23, *non* figs 19, 20.

STRATIGRAPHIC RANGE. Olenidsletta Member, V_1b, 8–19 m, above base.

MATERIAL. SM A105797, SM A105801, and several other incomplete specimens.

DESCRIPTION. The form differs from *Tetragraptus serra serra* mainly in its more robust rhabdosome. Details of development and proximal structure are unknown but the general aspect of the proximal region is like that of *T. serra serra*. Second-order stipes are more sharply flexed and more highly reclined and commonly have gentle (dorsally) convex curvature for the first 20 mm of their length. They widen at the same rate but reach a greater maximum width (4·4–4·7 mm, Fig. 17). Thecal spacing (9 in 10 mm) and curvature match those of *T. serra serra*.

DISCUSSION. The specimens are here separated from *T. serra* because they appear to lie just outside its field of variation. In view of the wide range of variation in stipe width described here in *T. serra,* however, it is possible that the full range of the species, when it is better known, will be found to include such forms; they are therefore here left in open nomenclature.

The specimens figured by Ruedemann (1947: pl. 50, figs 22, 23) from Idaho (zone not given) as *T. serra* match this Spitsbergen form well. *T. rigidus* Ge (1964) is a similarly rigid form but has more strongly reclined stipes and slightly more widely spaced thecae.

Tetragraptus (Tetragraptus) amii Elles & Wood 1902
Fig. 19a–f; Pl. 5, figs 6, 9

1865 *Graptolithus bryonoides* J. Hall; Hall *(pars)*: 84; pl. 4, figs 9, 10; *non* pl. 3, figs 11, 12; pl. 4, figs 1, 4, 6–8, ?11 (= *T. serra* Brongniart); *non* pl. 4, figs 2, 3 (= *T. toernquisti* Monsen).
1902 *Tetragraptus amii* Elles & Wood: 60–62; pl. 5, figs 4a–c (*ex* Lapworth MS).
1904 *Tetragraptus serra* (Brongniart); Törnquist: 8–10; pl. 1, figs 17–21.
1947 *Tetragraptus amii* Elles & Wood; Ruedemann: 301–302; pl. 50, figs 12–14.
1960 *Tetragraptus amii* Elles & Wood; Berry: 52; pl. 6, fig. 10; pl. 7, fig. 9.
1963 *Tetragraptus amii* Elles & Wood; Ross & Berry: 74–75; pl. 3, fig. 1.
1979 *Tetragraptus amii* Elles & Wood; Cooper: 60; pl. 7, fig. g.

LECTOTYPE. SM A17838, figured by Elles & Wood (1902: pl. 5, fig. 4b) and held in the Sedgwick Museum, Cambridge, is here designated **lectotype**.

STRATIGRAPHIC LEVEL. Olenidsletta Member, 49–87 m above base, V_1c–V_2a.

MATERIAL. PMO NF2817, NF3321–5.

DESCRIPTION. Sicula is 1·7 mm long but is seldom visible. First-order stipes are comprised of one theca each. Second-order stipes reach up to at least 23 mm long. They widen rapidly, as in *Tetragraptus serra,* reaching nearly their maximum width of 2·4 to 2·7 mm by the level of the 3rd or 4th theca. They are straight or have slight, dorsally concave, curvature. Divergence angle is highly variable in the flattened specimens from reclined to 'horizontal'. Rhabdosomes are very robust and the stipes often appear to have been buckled and rotated somewhat during preservation. Their original attitude is thought to have been gently reclined so that on flattening they generally splay out in a *quadribrachiatus*-like fashion (Fig. 19a). Immature rhabdosomes with short second-order stipes are often preserved with 'reclined' stipes (Fig. 19c).

Thecae are relatively straight and inclined at about 45° near their apertures. Apertural margins are deeply indented, giving a distinctively deeply serrated ventral margin to the stipe. They are spaced 11–13 in 10 mm in the proximal part of the stipe and 9–10 in 10 mm in the distal part.

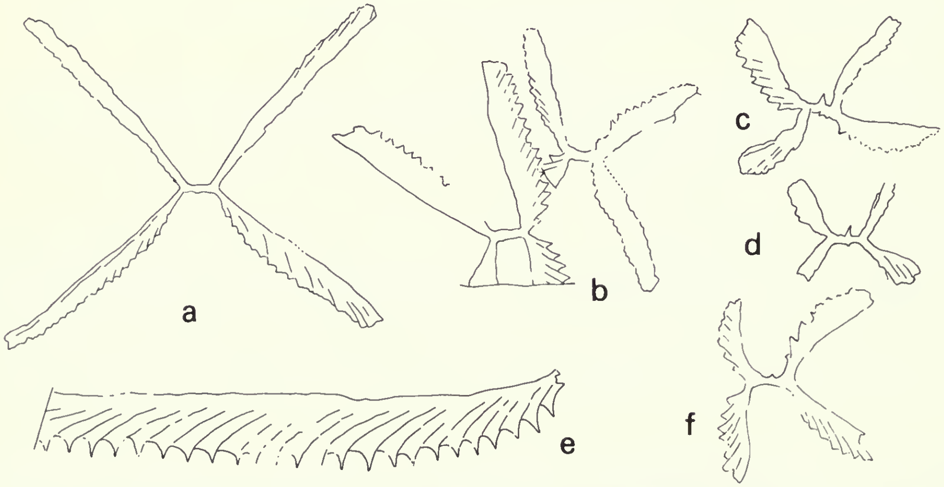


Fig. 19 *Tetragraptus (Tetragraptus) amii* Elles & Wood. a, PMO NF3324, complete mature specimen, in black shale band 49 m above base of Olenidsletta Member, southern section; × 2. b, two superimposed rhabdosomes, NF3323 below and NF3322 above, same horizon as a, × 2. c, NF3321, immature form, same horizon as a, × 2. d, NF3325, immature form, same horizon as a, × 2. e, NF2817, incomplete mature stipe preserved in full relief in limestone, 87 m above base of Olenidsletta Member, × 3. f, SM A109734, immature form attributable to either *T. (T.) amii* or *T. (T.) serra serra,* 40–43 m above base of Olenidsletta Member, type section; × 2·5.

DISCUSSION. Although Elles & Wood (1902) state that a maximum stipe width of 3·0 mm is most commonly met with, their figures (pl. 5, figs 4a–c) show that forms with more slender stipes (2·4–2·7 mm) were present, and it is with these more slender forms that the Spitsbergen material may be compared.

The distinction of *T. amii* from *T. serra serra* depends largely on its straighter and less strongly reclined stipes, and, less reliably, on its somewhat more slender stipes. When we can estimate the full range of variation of *T. amii* more reliably, it may be found to intergrade with that of *T. serra serra,* in which case its status as a distinct species would have to be reviewed.

Tetragraptus (Tetragraptus) bigsbyi (Hall 1865)

1865 *Graptolithus bigsbyi* J. Hall *(pars)*: 86–88; pl. 16, figs 25–26, 29, 30.
1964 *Tetragraptus hemirotundus* Ge: 384–385, 399; pl. 3, figs 7–13.
1965 *Tetragraptus bigsbyi* (Hall) Skevington: 4–8, figs 1, 3, 5, 6.
1979 *Tetragraptus bigsbyi* (Hall); Cooper: 62; pl. 8b, e; fig. 30.

STRATIGRAPHIC RANGE. 29–31 m above base of Olenidsletta Member, V_1b, early Arenig.

MATERIAL. SM A105798. Sedgwick Museum, Cambridge.

DESCRIPTION AND DISCUSSION. Although poorly preserved, the Spitsbergen specimen shows the characteristic small ovate rhabdosome outline with convergent second-order stipes of *T. bigsbyi.* The rhabdosome is 13 mm in length and 10 mm in width. Details of proximal development and structure are unknown. Second-order stipes are about 3·5 mm in maximum width which lies near the midpoint along their length. Thecae are spaced about 12 in 10 mm (6 in 5 mm).

The forms described as *T. hemirotundus* sp. nov. by Ge (1964: 399; pl. 3, figs 7–13) differ from *T. bigsbyi* only in having short (up to 6·5 mm long) second-order stipes. They may merely represent incompletely grown rhabdosomes. If the stated scale of the figured specimens is correct, then stipe width is nearer to 2·5–3 mm than to the 4 mm stated in the text. Ge's figured specimens best match those assigned to *T. bigsbyi* by Cooper (1979: 62; pl. 8b, e; fig. 30) which differ from Skevington's lectotype in their narrower (and shorter) second-order stipes. Since maximum stipe width is reached only near the midpoint of the stipes (at the 9th theca in the lectotype) incompletely grown rhabdosomes with shorter second-order stipes, such as those of China and New Zealand, are likely to attain a somewhat smaller maximum stipe width than that attained by mature rhabdosomes. For this reason, the Chinese and New Zealand forms are here included in the species.

Tetragraptus (Tetragraptus) cf. ***isograptoides*** Ge 1964

Fig. 20; Pl. 4, fig. 5

cf. 1964 *Tetragraptus isograptoides* Ge: 386–387, 400; pl. 3, figs 5–6; text-fig. 6.

STRATIGRAPHIC RANGE. 145 m (topmost Olenidsletta Member, V_3b) to top of Profilbekken Member (V_4a).

MATERIAL. PMO NF1810, NF1980, NF3252, NF3315.

DESCRIPTION AND DISCUSSION. In the uppermost part of the Olenidsletta Member (V_3b) and Profilbekken Member (V_4a) are several reclined tetragraptids, most of which are preserved in relief in limestone. No specimens are sufficiently complete to give a clear idea of

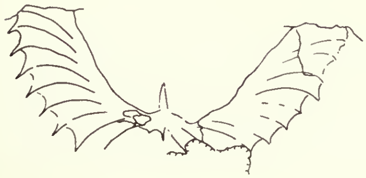


Fig. 20 *Tetragraptus (Tetragraptus)* cf. *isograptoides* Ge. PMO NF3315, showing a 1, 2 stipe pair. From Profilbekken Member, near V_4a/b boundary; × 4.

rhabdosome morphology and the following description is based on a number of incomplete specimens.

The rhabdosome is of *T. serra* type with gently to strongly reclined stipes. The sicula is about 2 mm or slightly more in length. Details of proximal development and structure are unknown. The second-order stipes are gently curved in the proximal region but become straight distally. They expand in width extremely rapidly, reaching almost their full width of 2·6–2·9 mm by the level of the second theca. Thecae are strongly curved as in *T. serra* and are spaced about 13–14·5 in 10 mm in the proximal region (measured over a stipe length of 6 to 7 mm).

The distinctive feature of the form is the rapid widening of second-order stipes, a feature which serves to distinguish the Spitsbergen material from most, otherwise similar, reclined tetragraptids, particularly *T. pseudobigsbyi.* The closest match for the Spitsbergen forms appears to be *T. isograptoides* Ge (1964: 400) described from the Ningkuo Shale of Zhejiang. From his description, Ge's species differs in its somewhat less closely spaced thecae (10 in 10 mm) and its short second-order stipes. However, because of the shortness of these stipes, estimates of thecal spacing (in 10 mm) can be derived only by extrapolating from the count in 3 or 4 mm of stipe length and are unlikely to be reliable. The short second-order stipes in the Chinese material (up to 5 mm long) more probably indicate the level of astogenetic development than constitute a reliable taxonomic character. Full sicula length (2·2 mm) in the Spitsbergen material is somewhat less than the 2·8 mm given by Ge for the Chinese material. But from Ge's figures, especially his text-fig. 6, the main difference in the Chinese form appears to be its more 'filled-in' proximal region giving it an unmistakable resemblance, as noted by Ge, to *Isograptus*.

Tetragraptus (Tetragraptus) phyllograptoides triumphans subsp. nov.

Figs 21, 22a–g; Pl. 4, fig. 3

STRATIGRAPHIC RANGE. 74·7–100·8 m above base of Olenidsletta Member, V_1c–V_3.

MATERIAL. **Holotype,** PMO NF771; paratypes PMO NF585, NF711, NF751(a + b), NF754, NF3182; isolated specimens NF3178–81.

NAME. 'Victorious', referring to the V-shaped rhabdosome.

DESCRIPTION. The sicula is 2·3 mm long; the supradorsal portion of the sicula and first theca form a prominent 'wedge', 1·3 mm high. The first-order stipes are short and formed of a single theca each. The second-order stipes are sharply flexed, becoming immediately reclined. The two pairs ($1^a + 1^b$, $2^a + 2^b$) are at first united along their dorsal margins but become separated distally so that when the rhabdosome is viewed from the side, the second-order stipes are seen to have a Y-configuration as in *T. phyllograptoides* Strandmark 1902, with an initial 'biserial' portion. In specimens from the 74·7 m level the two stipes are in contact as far as approximately the level of their 8th theca. Their dorsal margins, for a short distance thereafter, are bridged by a sheet of periderm. Stipes in the specimen from the 100·8 m level

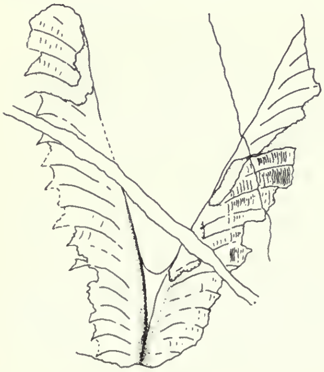


Fig. 21 *Tetragraptus (Tetragraptus) phyllograptoides triumphans* subsp. nov. PMO NF637, incomplete mature rhabdosome preserved in ¾ relief showing an a, b stipe pair. From 75 m above base of Olenidsletta Member; × 3.

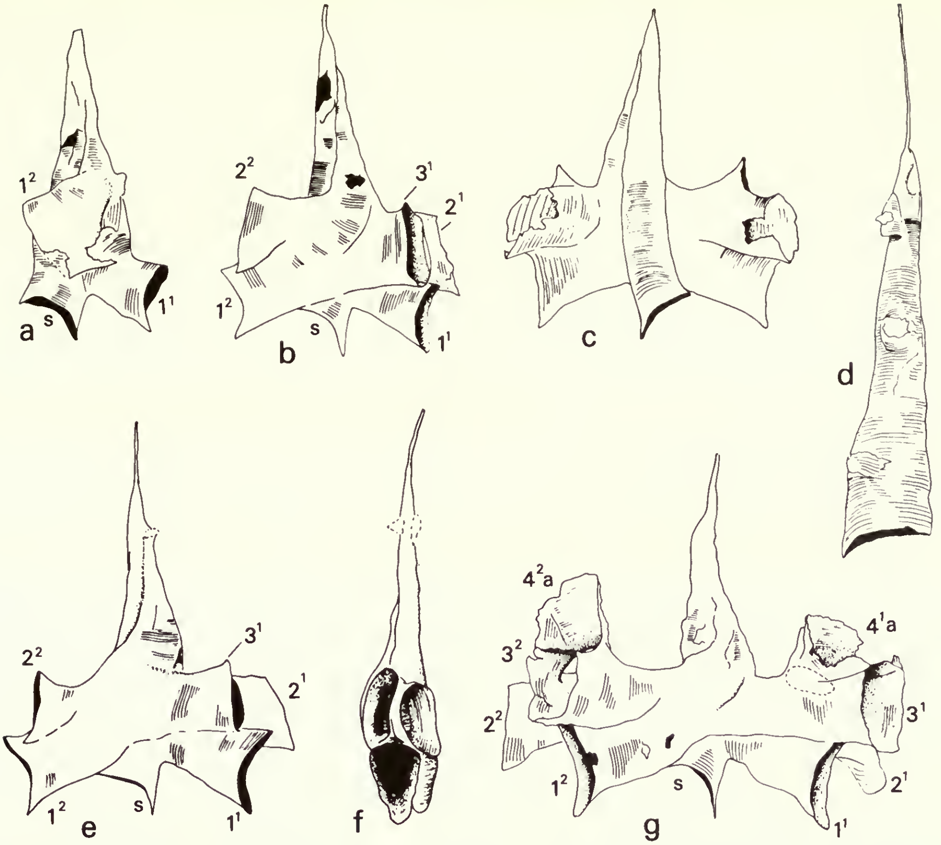


Fig. 22 *Tetragraptus (Tetragraptus) phyllograptoides triumphans* subsp. nov., growth stages. a, PMO NF3180 showing sicula, nearly complete th1^1 and beginnings of th1^2 and th2^1; × 20. b, c, NF3179 and NF3303 respectively, later stages (c, obverse view) showing commencement of growth of th2^1, 3^1 and 2^2; × 20. In c, note the wider spacing of fusellar rings in the lower wall of th2^1 on left, as compared with the closely spaced growth striations seen on the outer surface of all growth stages. d, NF3313, partially grown sicula and initial bud arising on the prosicula; × 40. e, f, NF3178, reverse and lateral (stipe^1 side) views respectively; × 20. g, NF3181, most advanced growth stage recovered, showing commencement of upward growth of second-order stipes; × 20. The foramen opening from th3^2 into th4^2b shows on left, and the position of the foramen between th3^1 and th4^1b is indicated on the right side of the diagram. The isograptid type of stipe division can be clearly deduced from this specimen. All from 74·7 m above base, Olenidsletta Member, type section.

(NF3182) are in contact up to at least the level of their 12th theca. The angle of divergence of the separated stipes is about 40°; the angle of intersection of the conjoined portions, as seen in transverse section, is about 120°.

Width of the second-order stipes near their origins is about 2·2 mm, at their point of separation about 3·4 mm and distally about 2·9 mm. Whereas the dorsal margin is convexly curved, the ventral margin is relatively straight, a feature also seen in *Oncograptus* and *Isograptus victoriae maximodivergens*. Maximum length of second-order stipes is over 17 mm.

Thecae are spaced 10–10·5 in 10 mm and are similar to those of *T. serra* from Spitsbergen.

PROXIMAL STRUCTURE AND DEVELOPMENT. Several growth stages have been isolated, of which six are figured (Fig. 22a–g). The apex of the prosicula passes gradually into a short nema or, possibly, the caudal region (Hutt 1974) of the prosicula.

The initial bud arises on the prosicula which is clearly defined in the earliest growth stage recovered (Fig. 22d) and is 0·25 mm in length. Proximal structure is similar to that of

Tetragraptus (Tetragraptus) bigsbyi (Bulman 1970: fig 53). Theca 1^1 grows down the ventral side of the sicula and turns sharply away leaving about 0·3 mm of ventral sicula wall exposed. The sicula aperture is deflected towards the stipe^2 side of the rhabdosome. Theca 1^2 arises from 1^1 at a point level with the sicula mid-length. It rapidly expands, and gives off th2^1, the proximal portions of the two thecae forming a broad structure on the reverse side of the rhabdosome as in *T. (T.) serra serra,* though less massive than in that species. The reclined growth of the second-order stipes is already apparent by the third-formed theca on each side (Fig. 22c, e), and strongly developed by theca 4 and 5 (Fig. 22g).

Thecal budding sequence can be clearly deduced from an advanced growth stage (Fig. 22g), and is identical to that of *T. (T.) bigsbyi.* The thecal diagram is given in Fig. 5a, b (p. 174).

Theca 1^2 is dicalycal and initial development is of isograptid type and dextral mode. In subsequent budding, th3^1 is dicalycal and right-handed, and th3^2 dicalycal and left-handed. Second-order branching is thus isograptid as in *T. bigsbyi* but second-order pairs of stipes remain united along their dorsal margins.

The thecal budding sequence (development) of the rhabdosome follows the pattern, not only of *T. bigsbyi,* but also of *T. reclinatus toernquisti, T. r. reclinatus, Pseudophyllograptus angustifolius angustifolius,* and *P. a. chors,* and can be regarded as the standard tetragraptid pattern.

Discussion. The distinctive rhabdosome form, with its two pairs of reclined second-order stipes united at their base, is shared only with one other described species, *T. phyllograptoides* Strandmark, known from the Baltic and Moscow Platform. Swedish forms of the species redescribed by Cooper & Lindholm (in prep.) differ from those of Spitsbergen in their greater number of pendent thecae in the proximal region. In other respects the Swedish form is apparently similar to that of Spitsbergen even to the distance for which the second-order stipes are united. In view of their difference in proximal morphology and of the fact that *T. phyllograptoides* is regarded as a zone fossil for a much lower horizon (zone of *T. phyllograptoides,* Törnquist 1901, Monsen 1937), it seems unwise to include the two forms under the one name. The new name *triumphans* is thus proposed for the Spitsbergen form which is here regarded as a stratigraphic subspecies of Strandmark's (1902) form.

If the partial concrescence of the second-order stipes were carried to completion the result would be a morphological intermediate between *Pseudophyllograptus* and *Tetragraptus,* and if this process were continued so that all four stipes were united the result would be a *Pseudophyllograptus* of *angustifolius* type. The appearance, in Spitsbergen, of *T. phyllograptoides triumphans* immediately before *P. angustifolius chors* subsp. nov. (p. 244) would be consistent with such a derivation for that form. However, the horizontal rather than downward initial growth of thecae 2^1 and 2^2 matches the later *P. angustifolius angustifolius* from Sweden (Bulman 1936*a*: fig. 15) more closely than *P. angustifolius chors,* so that the postulated transition would require some structural alteration in the proximal region in addition to change in rhabdosome structure.

Tetragraptus (Tetragraptus) pseudobigsbyi Skevington 1965

Figs 8a, 23a, b; Pl. 5, fig. 7

1865 *Graptolithus bigsbyi* J. Hall *(pars)*: 86–88; pl. 16, figs 22–24, 27, 28.
1964 *Tetragraptus bigsbyi* (Hall) Ge: 397–398; pl. 2, fig. 7?; pl. 3, figs 16–18.
1965 *Tetragraptus pseudobigsbyi* Skevington: 8–9, fig. 2.
1973 *Tetragraptus pseudobigsbyi* Skevington; Bouček: 20–22; pl. 1, fig. 1; text-figs 3e–g.
1976 *Tetragraptus bigsbyi* (Hall); Braithwaite: 28–29; pl. 5, figs 27–32; pl. 12, figs 1–4.

Stratigraphic range. Olenidsletta Member, 90·8–97 m above base, V_2a.

Material. PMO NF429, NF431, NF433, NF1580, NF3184.

Description. Rhabdosome of *T. serra* type, but with more strongly reclined stipes. Sicula 2·5 mm long, first-order stipes probably comprised of a single theca each. Details of proximal structure and development unknown. Stipes gently curved or straight distally,

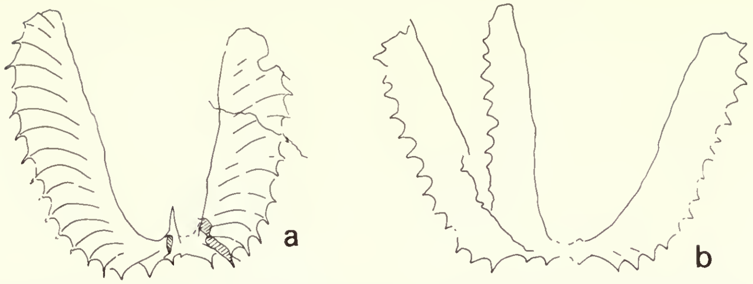


Fig. 23 *Tetragraptus (Tetragraptus) pseudobigsbyi* Skevington. a, PMO NF433, specimen preserved in full relief in limestone; 90·8 m above base, Olenidsletta Member, type section. b, NF3387, flattened specimen possibly belonging here, 22 m above base, Olenidsletta Member, type section. Both × 3.

3·5 mm in maximum width. Thecae of *T. serra* type, spaced 12–13 in 10 mm. Ventral processes protrude prominently, but are not always visible in rock-preserved relief material where they are commonly obscured by matrix.

Discussion. Skevington's (1965: fig. 2) figure of the holotype presents an a,b stipe pair and consequently proximal thecae with a higher angle of inclination than if preserved to show the first order stipes (and sicula) as in our Fig. 23a. In the absence of details of proximal development and structure, the species is distinguished from *T. serra* only in having slightly more strongly reclined stipes and more closely spaced thecae. It probably derived from earlier *T. serra* and should eventually, perhaps, be regarded as a stratigraphical subspecies of *serra*. Poorly preserved specimens from the Profilbekken Member (V_4) differ in having more slender stipes (2·8 mm) and are listed as *T.* cf. *pseudobigsbyi*.

T. pseudobigsbyi is distinguished from *T. bigsbyi* primarily in having less strongly reclined stipes that are straight or distally reflexed, and on these grounds the specimens described by Braithwaite (1976) from the Wahwah Limestone of early to mid-Arenig age, as *T. bigsbyi*, are here referred to *T. pseudobigsbyi*. Braithwaite described proximal development as isograptid, which might be expected from the close similarity of the species to *T. bigsbyi* in which isograptid development is well known (Bulman 1936*a*). The forms described as *T. bigsbyi* by Ge (1964), from the Ningkuo Shale of Zhejiang, eastern China, conform more closely with *T. pseudobigsbyi*; the main apparent difference is the wider thecal spacing in the Chinese specimens, given as 10–11 in 10 mm by Ge (1964: 397). However, as measured from his figured specimens, thecal spacing appears to be nearer to 12 in 10 mm.

Tetragraptus (Tetragraptus) reclinatus reclinatus Elles & Wood 1902

Figs 24a, b, 25a–f

1902 *Tetragraptus reclinatus* Elles & Wood: 67, fig. 41; pl. 6, figs 5a–e.

Lectotype. Specimen Q18, figured by Elles & Wood (1902: pl. 6, fig. 5e) and housed in the BM(NH) is here designated as **lectotype** (Fig. 24a).

Comments on type material. Although the species has been widely reported around the world, to our knowledge a lectotype has not previously been designated. We do so here in order to clarify the relationship of Elles & Wood's form to the new material from Spitsbergen. Of the several specimens they figured and now held by the BM(NH), that selected is the best preserved. Both the lectotype (Q18) and the specimen figured by Elles & Wood as pl. 6, fig. 5b (Q20) are refigured here (Fig. 24a, b).

Details of proximal structure cannot be seen in any of the type specimens. The sicula in the lectotype is about 1·8 mm long. The initial two thecae are slightly declined and the second order stipes grow out and up with graceful curvature, becoming straight distally and ending up with a gently reclined attitude. Longest stipes are 18 mm or more long. Stipes expand to their

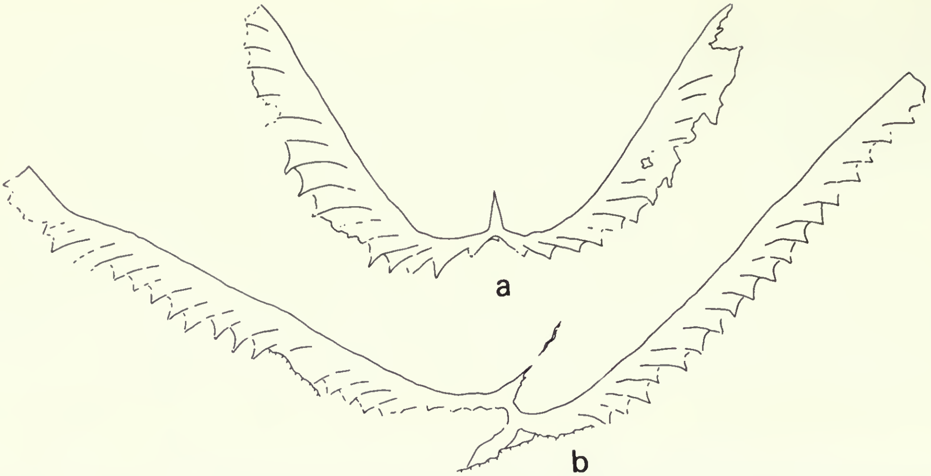


Fig. 24 *Tetragraptus (Tetragraptus) reclinatus reclinatus* Elles & Wood, type specimens. a, BM(NH) Q18, **lectotype;** b, Q20, paratype. Figured by Elles & Wood (1902: pl. 6, fig. 5e, 5b respectively). Both × 4.

full width of 2–2·5 mm by about their 7th or 8th theca (Fig. 29). It should be noted that several of the specimens figured by Elles & Wood, including the lectotype, lie outside the maximum value (2 mm) given by them for stipe width. Thecae are spaced 11–13 in 10 mm (12–13 given by Elles & Wood).

The species is distinguished from *Tetragraptus (Tetragraptus) amii* Elles & Wood (p. 198) by its shorter, more slender (Fig. 29) and less robust second-order stipes, and from *T. (T.) serra* Brongniart by these features and a shorter sicula, and less robust proximal region. Its astogeny is similar to that of *T. (T.) serra* and in morphology it can be regarded as a somewhat less robust version of Brongniart's species.

STRATIGRAPHIC RANGE. 74·7 m level, upper V_1c, Olenidsletta Member.

MATERIAL. PMO NF3304–8.

PROXIMAL STRUCTURE AND DEVELOPMENT. The sicula is 2 mm long, straight and bears a well-developed ventral prolongation of the apertural margin. The preservation is not good enough to allow the prosicula to be distinguished, but a tubular structure, either the cauda or nema, extends from the sicular apex. In the earliest growth stage recovered (Fig. 25a) theca 1^1 arises high on the ventral side of the sicula and grows down in contact with the sicula, then diverges sharply leaving free about 0·25 mm of the ventral sicula wall. The level of origin of th1^2 and the foramen to th2^1 can be seen in Fig. 25a. From the unconformity in growth striations it is inferred that th1^2 commences its growth in the form of a dorsal hood, like that of *Xiphograptus formosus formosus* (Bulman 1936a: 24; Skevington 1965: 20) and *X. formosus svalbardensis* (Archer & Fortey 1974: 93). The hood is later linked to the ventral wall (of th1^2 and 2^1) by fuselli which join it at a relatively high angle. Theca 2^1 grows out over the dorsal wall of th1^1 to open on the obverse side of the rhabdosome; th2^2 also opens on the obverse side. Subsequent development follows the usual tetragraptid plan, as in *T. bigsbyi, Pseudophyllograptus angustifolius* etc. Initial development is thus of dextral mode and isograptid type; th3^1 is dicalycal and right-handed, th3^2 is dicalycal and left-handed.

LATER GROWTH STAGES. The most complete growth stage is a rhabdosome fragment (Fig. 25e, f) comprising the proximal region and one incomplete stipe. It is sufficient to show that the second-order stipes are gently reclined. Maximum width of the incomplete stipe is 2 mm at the 4th theca. Apertural margins are deeply indented; thecae are moderately curved so that their free ventral margins are inclined to the dorsal stipe margin at 70°–80°.

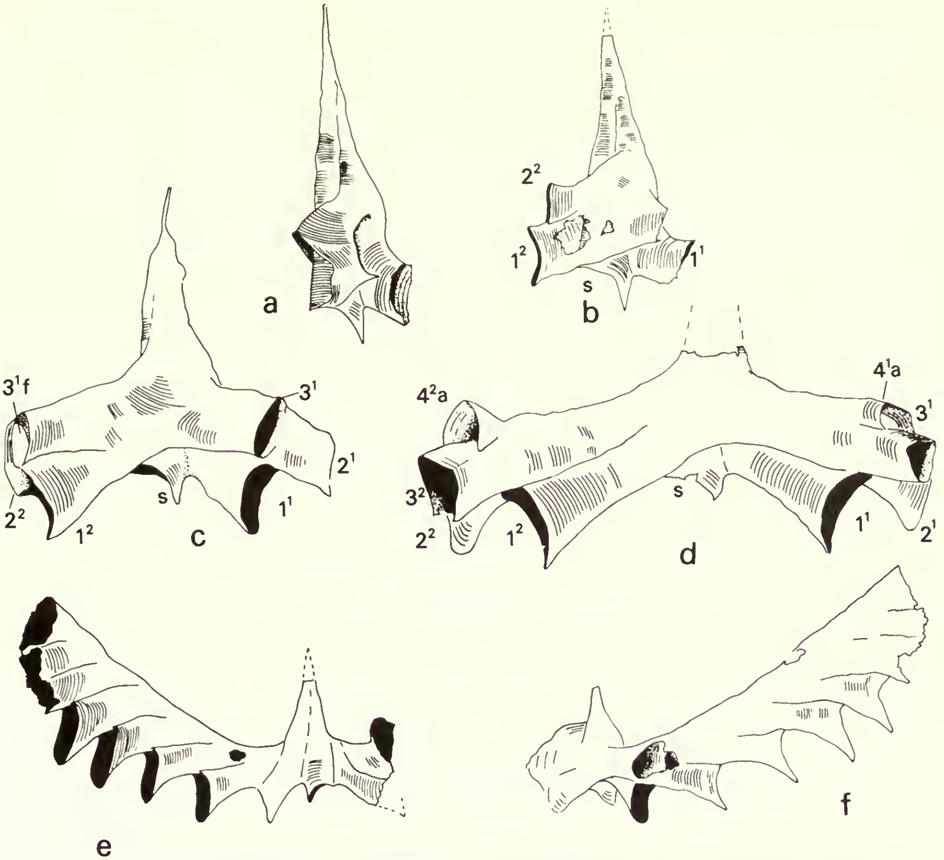


Fig. 25 *Tetragraptus (Tetragraptus) reclinatus reclinatus* Elles & Wood, isolated growth stages from Spitsbergen in which growth of thecae can be inferred from growth striations. a, PMO NF3308, earliest stage showing sicula, partly grown th1^1 and incipient development of th1^2, with a wide foramen from which th2^1 would develop; × 20. The unconformity in growth lines shows clearly. b, NF3307, stage showing the commencement of growth of th2^1 (damaged), and th2^2; × 20. c, NF3305, later stage in which the wide foramina opening into th3^1 and th3^2 (3^2f) are clearly displayed; × 20. d, NF750, advanced growth stage from which the budding sequence of the two second-order dichotomies can be inferred; × 20. e, f, NF3305, obverse and lateral-reverse view of proximal region with proximal portion of stipe ^{1}a; × 10. All from 74·7 m above base of Olenidsletta Member, type section.

Discussion. Although incomplete, the Spitsbergen material is referred to Elles & Wood's species because of its gently reclined stipes and closely comparable stipe expansion rate (Fig. 29). The species' range of morphologic variation is unknown and it is not possible to assess the significnce of slight differences in dimensions and curvature in otherwise similar described tetragraptids such as those figured by Cooper (1979: fig. 35). However, the specimens described by Skevington (1965: 10–14) as *T.* cf. *reclinatus* and *T.* cf. *serra* have stipes which appear to expand more rapidly than those of *T. reclinatus* as described here.

Tetragraptus (Tetragraptus) cf. *reclinatus reclinatus* Elles & Wood 1902
Fig. 26a, b; Pl. 4, fig. 11

cf. 1902 *Tetragraptus reclinatus* Elles & Wood: 67; pl. 6, figs 5a–e.

Stratigraphic range. Olenidsletta Member, 22 m above base, V$_1$b.

Material. PMO NF2791, NF3188; flattened specimens.

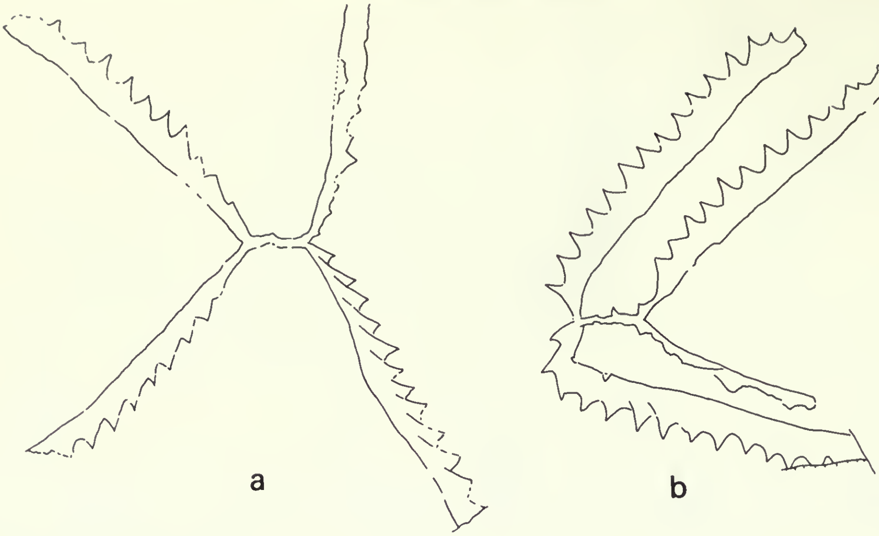


Fig. 26 *Tetragraptus (Tetragraptus)* cf. *reclinatus reclinatus* Elles & Wood, flattened rhabdosomes. a, PMO NF3188; b, NF2791. Both from Olenidsletta Member, 22 m above base, southern section; × 3.

Description. The sicula is small but its dimensions are unknown. The first-order stipes form a funicle 2·3 mm long. Second-order stipes are up to 18 mm long, straight or slightly curved, concave dorsally. They appear to have been gently reclined so that, as in *T. amii*, they are sometimes preserved in quadribrachiate mode (Fig. 26a) and others in *serra* mode. Stipes reach their maximum width of 1·9–2·0 mm by about their 5th theca. Thecae are moderately curved, and free ventral margins are inclined 50°–70°. Apertural margins are deeply indented and relatively straight, leaving free a relatively large portion of the ventral wall of the following theca. The ventral stripe margin thus has a characteristically deeply serrated outline.

Discussion. The distinctive feature of the Spitsbergen forms is their deeply serrated stipes, and separates them from other tetragraptids of similar rhabdosome form, such as *T. reclinatus reclinatus* Elles & Wood, *T. r. toernquisti* Monsen (both of which also differ in having more closely spaced thecae), *T. ibexensis* Braithwaite (?= *T. reclinatus* Elles & Wood), *T. amii* Elles & Wood (which also has broader and more rapidly widening stipes) and *Tetragraptus woodae* Ruedemann. There appears to be no suitable name for the Spitsbergen form but the poor quality of our specimens precludes their being used as the basis of a new species. Since they most closely match Elles & Wood's *T. reclinatus* they are listed here as *T.* cf. *reclinatus.*

Tetragraptus (Tetragraptus) reclinatus abbreviatus Bouček 1956
Fig. 27

1956 *Tetragraptus (Tetragraptus) reclinatus abbreviatus* Bouček: 26; pl. 1, figs 2, 3; text-fig. 8a–d.
1973 *Tetragraptus reclinatus abbreviatus* Bouček; Bouček: 22–23; pl. 2, figs 5–7; text-fig. 3a–d.

Stratigraphic range. Olenidsletta Member, 20–21 m above base, V_1b.

Material. PMO NF2392, NF3187.

Description and discussion. Small, strongly reclined tetragraptids. Sicula prominent, 2·3 mm long; first-order stipes composed of a single theca each. Second-order stipes 7 mm long and 2·1 mm in maximum width. Thecae are strongly curved, and their free distal margins are inclined at about 90° to the stipe axis. The apertural margins are deeply indented and form an

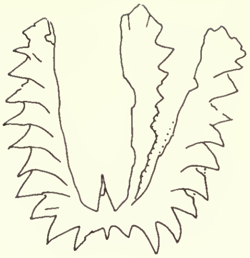


Fig. 27 *Tetragraptus (Tetragraptus) reclinatus abbreviatus* Bouček. PMO NF2392, 20–21 m above base of Olenidsletta Member, southern section; × 4.

acute angle with the ventral margin, giving a characteristic deeply serrated outline to the ventral stipe margin.

The Spitsbergen specimens match Bouček's figures and description well and correspond with the wider-stiped forms in his population. Bouček's material comes from the uppermost layers of the Klabava Formation (*T. reclinatus abbreviatus* Zone) in beds correlated with the late Arenig, that is, a horizon somewhat higher than that of the Spitsbergen material.

Tetragraptus (Tetragraptus) reclinatus toernquisti Monsen 1937
Fig. 28a–m

1937 *Tetragraptus törnquisti* Monsen: 161–162; pl. 3, fig. 31; pl. 4, figs 27, 33; pl. 13, figs 1–3.

STRATIGRAPHIC RANGE. 103·3–131 m above base of Olenidsletta Member, V_2b–V_3.

MATERIAL. PMO NF3189, NF3296–3302, NF3316–8, and numerous other fragmentary specimens, all isolated and in full relief, strongly carbonized; growth lines were revealed in some specimens which partly responded to bleaching in potassium chlorate and nitric acid. PMO NF3221, preserved in shale.

PROXIMAL STRUCTURE AND DEVELOPMENT. The sicula is generally 1·6–1·7 mm long and 0·31–0·33 mm in dorsoventral width at the aperture. It is straight for most of its length; the distal portion, that below the point at which th1^1 diverges, is slightly curved towards the dorsal side. The ventral margin of the aperture projects slightly beyond the dorsal margin. Preservation is too poor to allow distinction of the prosicula. Theca 1^1 arises very high on the sicula, follows the same growth path as in *T. reclinatus reclinatus* but diverges from the sicula less sharply. Theca 1^2 commences its growth as a dorsal hood like that inferred for *T. reclinatus reclinatus*. At the same time the lower wall, bridging th1^2 and 2^1 (that forming the isograptid arch), is formed as a shelf or plate against the sicula and th1^1 (Fig. 28a). The hood apparently ceases growth and the lower shelf is extended up to meet it; at the same time the distal margin of th1^2 becomes fully enclosed by the formation of complete half rings. A deep embayment is thus formed (Fig. 28b, c) which eventually is filled in during the formation and growth of th2^1. The growth path of th2^1 differs from that of its homologue in *T. reclinatus reclinatus* by passing across the sicula and th1^1 at a lower level, its ventral wall lying at the level of the junction of the free ventral walls of the sicula and th1^1. Subsequent development follows that of the nominate subspecies; th3^1 is dicalycal and right-handed and th3^2 is dicalycal and left-handed. Initial development is of dextral mode and isograptid type.

LATE GROWTH STAGES. The first-order stipes and proximal parts of the second-order stipes are slightly declined. Second order stipes have similar graceful proximal curvature and gently distally reclined attitude to those of *T. reclinatus reclinatus*. They are proportionately narrower than those of *T. reclinatus reclinatus* (Fig. 29), reaching a width of 1·8–2·1 mm by the 7th or 8th theca, but expand at the same rate. The longest stipe measured is 24 mm long. Thecae are spaced 11–13 in 10 mm in the proximal part of the stipe and slightly wider (down to 10·5 in 10 mm) in the distal part. Thecae are similar in outline and inclination to those of *T. reclinatus reclinatus*.

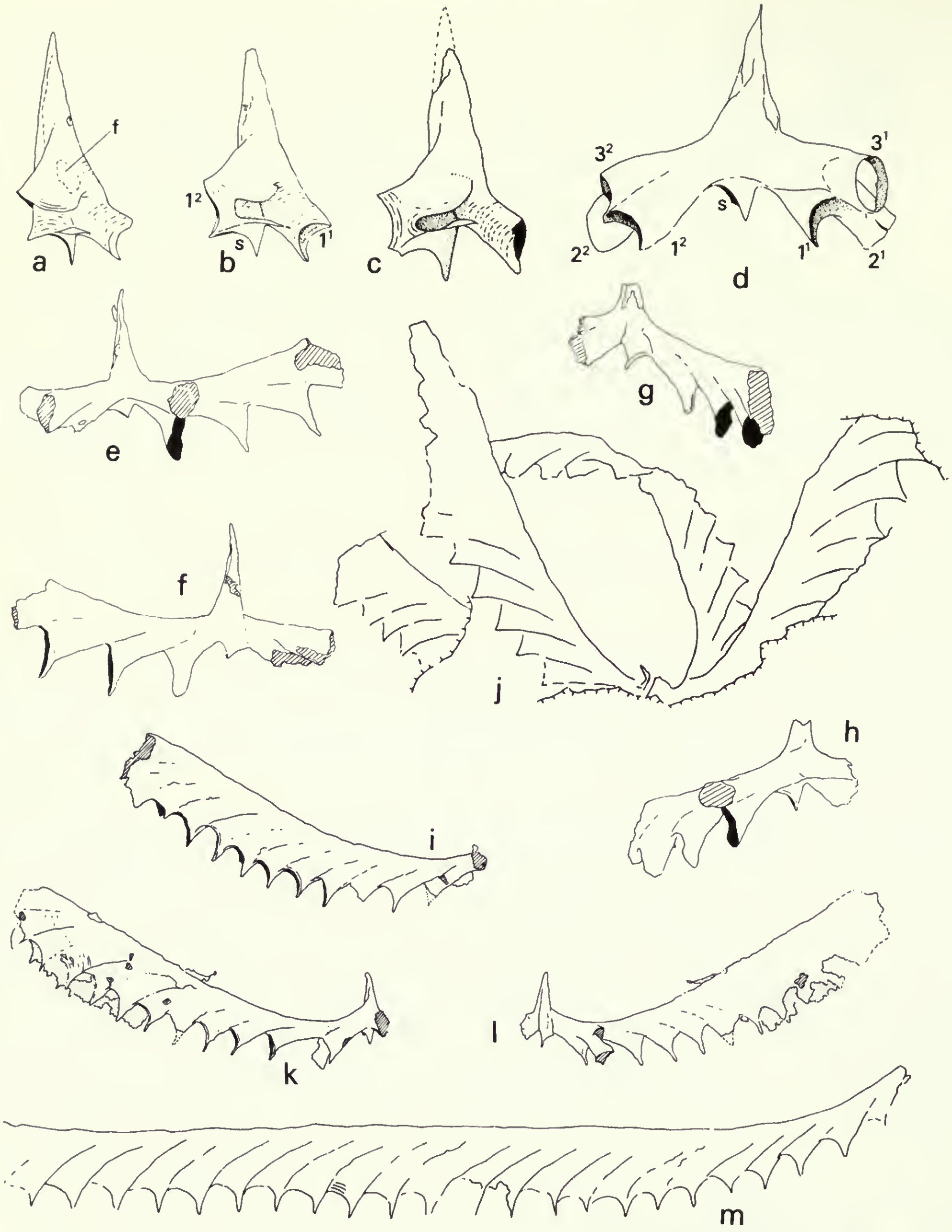


Fig. 28 *Tetragraptus (Tetragraptus) reclinatus toernquisti* Monsen, isolated growth stages and rhabdosome fragments. a–c, PMO NF3299, NF3298 and NF3317 respectively, successive growth stages showing formation of hood over th1^2 and 2^1, lower 'shelf', and deep embayment formed between these two structures (c), some fuselli visible; × 20. d, NF3301, commencement of second-order dichotomies with dicalycal thecae 3^1 and 3^2 beginning to form; × 20. e, f, NF3297, incomplete proximal end, reverse and obverse views; × 10. g, h, NF3316, incomplete proximal end, obverse and reverse views; × 10. i, NF3318, isolated second-order stipe; × 6. j, NF3221, flattened rhabdosome in shale; × 6. k, l, NF3296, proximal region and stipe ^{2}a viewed from reverse side and obverse side respectively; × 6. m, NF3189, incomplete second-order stipe preserved in full relief in limestone; × 6. All from 103·3 m level, Olenidsletta Member, type section, except specimen j which is from 131 m above base of Olenidsletta Member, southern section.

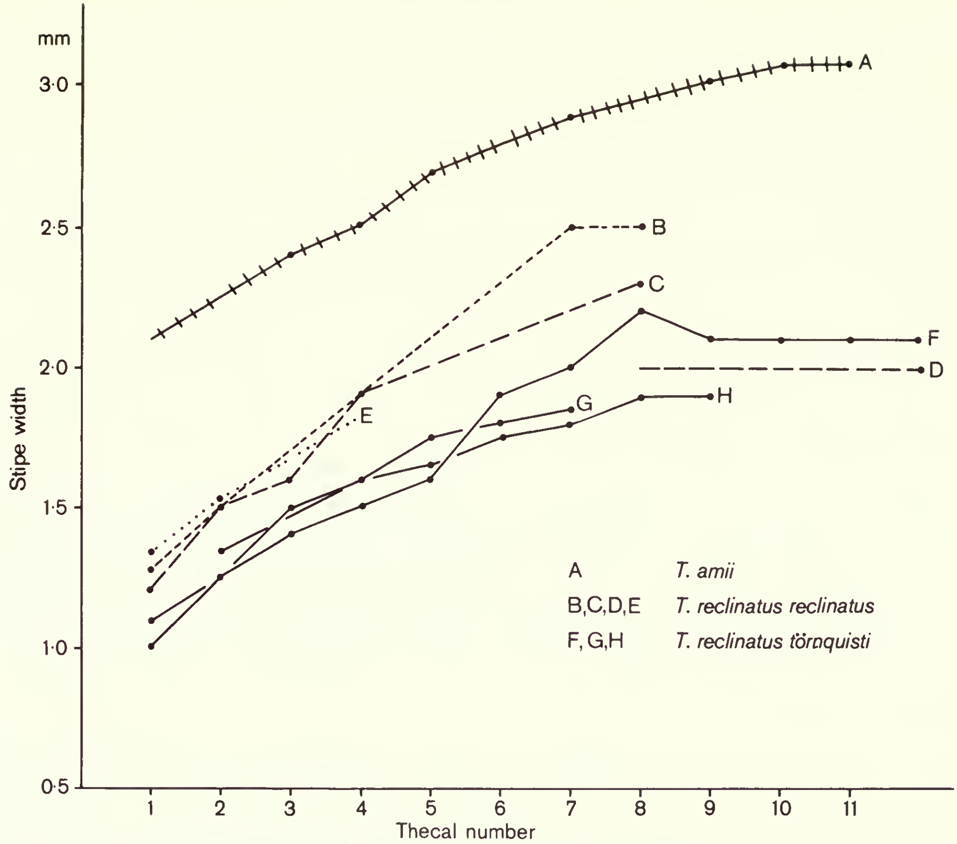


Fig. 29 Stipe expansion curves for second-order stipes of *Tetragraptus (Tetragraptus)* species. A, *T. (T.) amii,* PMO NF2817, from Spitsbergen. B–E, *T. (T.) reclinatus reclinatus.* B, lectotype (BM(NH) Q18); C, paralectotype (BM(NH) Q19); D, paralectotype (Q20), measurements obtainable in distal part only; E, specimen from Spitsbergen (NF3305). F–H, *T. (T.) reclinatus toernquisti,* from Spitsbergen. F, NF3189; G, NF3296; H, NF3318. Note that specimens A–D are flattened (shale material), whereas specimens E–H are preserved in relief (isolated material).

Discussion. The subspecies is represented by abundant stipe fragments in our acid-insoluble residues from the 103·3 m level. Most appear to be broken off the rhabdosome shortly after the second dichotomy. Only a single specimen (Fig. 28j) was found preserved in black shale.

The form differs from that referred to *T. reclinatus reclinatus* in the lower level of its isograptid arch, in the slightly narrower stipes and in its higher stratigraphical position, but there seems little doubt that the two subspecies are closely related.

Monsen's (1937) description of *Tetragraptus toernquisti* is, unfortunately, based on flattened material. From her illustrations the species possessed slightly reclined stipes which become straight distally, rather than horizontal stipes. She gives the following dimensions: stipe width initially 0·4 mm but 'rapidly increasing' to about 1·6 mm; in one example, with stipes 17 mm long, stipe width reaches about 2 mm; thecae are spaced 11–14 in 10 mm. The low value given for proximal stipe width can be expected in flattened shale-preserved material where the full dorsoventral profile of the proximal part of the stipe is not usually seen.

The Spitsbergen material thus appears to best fit Monsen's descriptions and illustrations of *T. toernquisti.*

Among the isolated stipe fragments recovered from samples taken at the 103·3 m level are some which differ from the main population in being somewhat thinner. Whether they represent a separate population or are merely the thinnest variants of a single variable population is uncertain; they are separated under the name *T. reclinatus* cf. *toernquisti*.

Subgenus *PENDEOGRAPTUS* Bouček & Přibyl, 1951

TYPE SPECIES. *Tetragraptus pendens* Elles 1898.

DIAGNOSIS. Sicula long, slender, wedge-shaped, first theca almost straight, all proximal thecae pendent and proximal region of bryograptid appearance; thecae with projecting ventral apertural margins; up to three orders of consecutive dichotomy, variable in some species.

SPECIES. *Tetragraptus pendens* Elles 1898, *Graptolithus fruticosus* J. Hall 1858, *Tetragraptus clarki* Ruedemann 1902 (?= *T. (P.) fruticosus*), *T. pendens* mut. *posterus* Ruedemann 1947 (= *T. (P.) pendens*), *T. fruticosus* var. *tubiformis* Ruedemann 1904 (= *T. (P.) fruticosus*), *T. fruticosus* var. *campanulatus* Ruedemann 1904 (= *T. (P.) fruticosus*), *T. pendens* var. *praesagus* Törnquist 1901 (?= *T. pendens*), and *Bryograptus crassus* Harris & Thomas 1938.

DISCUSSION. The diagnosis is based on *Tetragraptus fruticosus* (Hall). Until the diagnostic features are confirmed in the type species (*T. pendens* Elles) it, and the subgenus itself, remain provisional. The species here included are confined to strata of Lower Arenig age. Four terminal stipes are the general rule but at least one species, *T. (Pendeograptus) fruticosus,* produces polymorphic variants by the suppression of first one second-order dichotomy (to produce a three-stiped form) and then the second second-order dichotomy (to produce a two-stiped form). Development type has been inferred only in *T. (Pendeograptus) fruticosus* where initial development is dextral and isograptid, and subsequent development, inferred with less confidence, follows the plan of *Tetragraptus (Tetragraptus).*

The bryograptid appearance of the proximal region of *T. fruticosus* has long been recognized and its derivation from a bryograptid ancestor has been suggested (Elles 1922; see also Ruedemann 1904, Obut 1957). In the *T. (P.) fruticosus* beds of Victoria is found the closest relative of the species, *Bryograptus crassus* Harris & Thomas (1938: 72–73; pl. 1, figs 7a–d; pl. 4, fig. 6). The sicula and thecae are said to be of the same type as those of *T. fruticosus* and (flattened) growth stages of the two forms cannot be distinguished from each other. In *Bryograptus crassus* dichotomies are taken to the third order; the number of terminal stipes ranges from four to six, the four-stiped forms being indistinguishable from slender four-stiped *T. (P.) fruticosus*. Harris & Thomas (1938: 72) state '. . . the species seems so closely related to *T. fruticosus,* which occurs in the same bed, that one cannot resist the conclusion that the two forms are genetically related although according to the artificial classification in use they must be placed in different genera'.

Although their figures show that details of proximal structure and sicular morphology are not preserved in the Victorian material, their conclusions concerning relationships seem justified. *B. crassus* is therefore here included in the subgenus *Pendeograptus* and the diagnosis of *Pendeograptus* is framed accordingly. Bithecae are unknown in *B. crassus* and its inclusion in *Bryograptus* was clearly based on the number of terminal stipes and the bryograptid character of the proximal region, thecae, and rhabdosome. The stratigraphic range is given by Thomas 1960 as Lower Bendigonian (Be1), equivalent to the lower part of the range of the four-stiped *T. fruticosus.*

Tetragraptus (Pendeograptus) fruticosus (J. Hall 1858)

Fig. 30a–f; Pl. 3, fig. 4; Pl. 4, fig. 2

1858 *Graptolithus fruticosus* J. Hall: 128.
1865 *Graptolithus fruticosus* Hall; J. Hall: 90–91; pl. 5, figs 6–8; pl. 6, figs 1–3.
1874 *Graptolites (Didymograptus) fruticosus* (Hall) M'Coy: 13; pl. 1, figs 9–14.
1874 *Didymograptus pantoni* Etheridge: 7; pl. 3, figs 21–22.
1902 *Tetragraptus fruticosus* (Hall) Elles & Wood: 61; pl. 6, figs 2a–b.
1935 *Tetragraptus fruticosus* (Hall); Benson & Keble: 275–276; pl. 30, fig. 41; pl. 33, figs 25, 27.
1947 *Tetragraptus fruticosus* (Hall); Ruedemann: 304–305; pl. 51, figs 25?, 26–32.

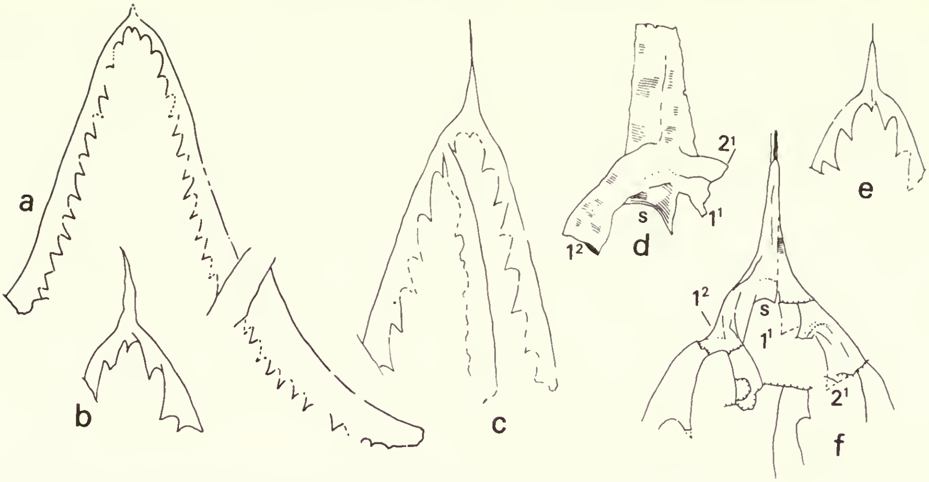


Fig. 30 *Tetragraptus (Pendeograptus) fruticosus* (Hall). a, PMO NF3325, mature two-stiped form, 15–24 m above base of Olenidsletta Member, southern section; × 2. b, NF2836, proximal portion only, 11 m above base of Olenidsletta Member; × 4. c, NF3327, three-stiped form, 9·5–15 m above base of Olenidsletta Member, southern section; × 4. d, SM A105809, incomplete growth stage showing origin of th2^1 on 1^2, isolated but flattened specimen; same horizon as a; × 20. e, NF2852, proximal portion, 18–19 m above base of Olenidsletta Member, southern section; × 4. f, pyritized specimen in shale in partial relief, showing some details of proximal development and structure; from Newfoundland; × 6.

1960 *Tetragraptus fruticosus* (Hall); Berry: 54–55; pl. 6, figs 7, 11, 12; pl. 7, fig. 14; pl. 8, figs 1, 3; pl. 9, fig. 3.
1960 *Tetragraptus fruticosus* (Hall); Thomas: pl. 3, figs 26–28.
1979 *Tetragraptus fruticosus* (Hall); Cooper: 64–65; pl. 6b, e, g; figs 32a–c.

Stratigraphic horizon. Olenidsletta Member, 13–19 m above base, V_1b (both two- and three-stiped forms).

Material. SM A105809(?), PMO NF2075, NF2836, NF2852, NF3325–7.

Description. The sicula is long and wedge-shaped, ranging from 2·5 to 3·5 mm in length (measured in five specimens). The apex is often difficult to determine, passing smoothly into a nema. The rhabdosome comprises either two or three main stipes – no four-stiped forms are present in the Spitsbergen collections. In the three-stiped form, one first-order stipe (whether stipe^1 or stipe^2 could not be determined) bifurcates after its first theca to produce two second-order stipes, whereas in the two-stiped form both first-order stipes remain unbranched. The terminal stipes show considerable variation in width and curvature. Most specimens have stipes that are pendent, more than about 2 mm in maximum width, and are no more than about 14 mm in length. A few have long stipes that continue to expand in width, reaching 3·6 mm at about theca 15 (25 mm from the proximal end), thereafter tapering gradually; stipes are reflexed giving the rhabdosome the characteristic bell shape noted by Hall. It is not clear from the Spitsbergen material whether the specimens with shorter slender stipes represent a distinct form or are merely immature growth stages of the larger form. Both forms have two- and three-stiped representatives.

Thecae are strongly denticulate, with deeply recessed apertural margins, resembling in outline those of dendroids. They are spaced 7 to 8 in 10 mm.

Proximal development. A few isolated, but flattened, growth stages have been recovered that may represent the species, one of which is figured (Fig. 30d). If correctly assigned it is important because it reveals some details of proximal development. The apices of the sicula and first theca have broken off but origin of th1^2 and its initial path of growth are clear. Theca 2^1

originates from 1^2 but it is broken off shortly after its origin along with the distal portion of th1^1. The fragment thus shows dextral development of isograptid type, in agreement with that deduced in the Newfoundland specimen described below.

Description of Newfoundland specimen. A specimen of the slender form of *T. fruticosus* (four-stiped) has been collected from the Cow Head Group of Newfoundland by one of us (R.A.F.) and its description is included here for completeness (Fig. 30f) since it is preserved in partial relief and shows details of proximal development. The sicula is 2·8 mm long, wedge-shaped, and terminates apically in a slender nema which appears to be enveloped in a membrane. Width of the membrane is similar to that of the sicula near its apex. There is no pronounced virgellar projection at the aperture and the ventral side of the sicula is not defined. Theca 1^1 originates high on the sicula, but its point of origin cannot be determined. It is relatively straight, diverging from the sicula at a very low angle, and its aperture lies 0·6 mm below that of the sicula.

The periderm has flaked away in the proximal region of our specimen and the following interpretation is based on the impression remaining, together with the periderm still preserved.

Theca 1^2 arises from th1^1 about 0·8 mm above the aperture of the sicula; it grows aross the sicula and down assuming a pendent attitude, its aperture lying beneath, and obscured by, the bifurcation of stipe^2. Theca 2^2 arises from th1^2 in the region of the sicula aperture and follows a sinuous growth path (probably accentuated by flattening of the rhabdosome). The origin of th2^1 is not preserved but from an impression in the lower part of the sicula it is probable that a second 'crossing canal' was present and th2^1 is therefore likely to have originated from th1^2 rather than from th1^1.

Subsequent development of the rhabdosome is a little obscure and two interpretations are possible for the origin of second-order stipes on both the stipe^1 and stipe^2 sides. In the most probable interpretation for the stipe^1 side, th2^1 grows out along the right-hand stipe shown in Fig. 30f, th3^1 is dicalycal and th4^1b is given off producing a dichotomy that is right-handed and isograptid. However, because the origin of th3^1 is not clearly defined, it is possible that the growth path of th2^1 is misinterpreted above, and that instead it grows along the left-hand stipe; th2^1 would then be the dicalycal theca and the dichotomy would be of *artus* type.

Similarly, on the stipe^2 side, the most probable interpretation is that th3^2 is given off from th2^2 at the level of the aperture of th1^2; it grows out along the left-hand stipe shown in Fig. 30f, and is dicalycal, giving rise to th4^2b which grows down the right hand stipe, thus producing a dichotomy that is of isograptid type (whether of right- or left-handed mode is uncertain). A possible, but less probable, interpretation would have th2^2 as dicalycal, producing a dichotomy of *artus* type.

In the favoured interpretation, development of the rhabdosome follows the general plan of other tetragraptids with all dichotomies of isograptid type and dicalycal thecae separated, in budding succession, by normal unicalycal thecae. However, should either, or both, of the alternative interpretations for the two second-order dichotomies hold true, then *T. fruticosus* would depart significantly from the general tetragraptid plan, and occupy a unique place among the dichograptids in having first isograptid, then *artus* type dichotomies in succession (see, however, *Didymograptus (Didymograptellus) multiplex* sp. nov. described below, p. 229).

Discussion. The significance of the two rhabdosome forms, that with pendent narrow stipes and that with broad reflexed stipes, is not clear. Hall's (1865) illustrations show that both forms were present in his material and both forms are present in Australia (Thomas 1960) and New Zealand (Cooper 1979). It is clear that in some cases at least (e.g. the New Zealand material) the slender form could not represent an immature stage of the broad reflexed form, since its stipes are pendent and straight beyond the point of reflection in the reflexed form. However, from the literature, there appears to be considerable variation in the level at which the stipes become reflexed. In the New Zealand form (Cooper 1979: fig. 32a, 4-stiped) they commence their recurvature at about the level of th8–9, in the Australian form of Thomas (1960: pl. 3, fig.

28a, 3-stiped) at about th11–12, in New York specimens of Ruedemann (1947: pl. 51, figs 26–32) at th11–12 (in 3- and 4-stiped forms referred to 'variety *tubiformis*') and th20–24 (3- and 4-stiped forms of 'variety *campanulatus*'), and in Quebec specimens of Hall (pl. 6, figs 1–3, 3- and 4-stiped) at about th12–14. Pending a review of the species all forms are here retained within it.

Two-stiped forms of *T. fruticosus* have long been known in Australia (Etheridge 1874, Thomas 1960) but to our knowledge have not been recorded from elsewhere. However, they are closely similar to the forms described as *Didymograptus v-fractus* Salter by Elles & Wood (1902: 33–35; pl. 2, figs 10a–b) and may well be present elsewhere recorded under Salter's name. The two species are certainly closely similar. From their description and illustrations Elles & Wood's material differs in having a somewhat shorter sicula (2–2·5 mm), slightly more closely spaced thecae, stipes that do not attain the full width of 3·5 mm of the broad reflexed *T. fruticosus,* and apertural margins that are less recessed resulting in less conspicuously denticulate thecae. However, the question needs further examination before the relationship between the two forms can be assessed.

Etheridge (1874) figured Victorian specimens of the two-stiped form under the name *Didymograptus pantoni*? M'Coy, and listed in his synonymy of *D. pantoni* a reference to Salter 1863. In fact neither M'Coy nor Salter figured or described the form and authorship of the name *pantoni* must be attributed to Etheridge. The name has not generally been used by subsequent Australasian workers (e.g. Keble & Benson 1939, Thomas 1960) who have regarded it as a synonym of *T. fruticosus* (Hall).

In Australia and in Spitsbergen, the two-stiped form has a similar range to that of the three-stiped form. The two-stiped form can be derived from the three-stiped form by suppression of the second dichotomy. Although not clear in the Spitsbergen material, the third-formed stipe in three-stiped forms was found to be developed on the stipe^1 side in New Zealand material (Cooper 1979) and the three-stiped form was thus regarded as being derived from the four-stiped form by suppression of the last dichotomy (that based on stipe^2). It therefore follows that all three forms (two-, three-, and four-stiped) of *T. fruticosus* can be regarded as polymorphic variants of a single species (Cooper 1979: 64) in which there is a change in morph frequency with time; four-stiped forms appear first, then two-, three- and four-stiped forms together, and two- and three-stiped forms only are found at the top of the range. The change in frequency with time has been employed for stratigraphic subdivision of early Arenig sequences (Thomas 1960, Berry 1960, 1962).

TETRAGRAPTUS Salter 1863, *sensu lato*

Tetragraptus contrarius sp. nov.

Fig. 31a–d; Pl. 3, figs 2, 3

STRATIGRAPHIC RANGE. Mid-part of Olenidsletta Member, V_2, 90–97 m from base; top of the Arenig *Didymograptus bifidus* Zone (Ca_1).

DIAGNOSIS. Robust, reflexed *Tetragraptus* with mature stipe width 4–6 mm. Strong dorsal-convex curvature of stipe unique among tetragraptids, producing long thecae with initially low inclination, highly curved distally, and overlapping as far as long apertural lips. Distal thecal spacing 10–12 in 10 mm.

MATERIAL. **Holotype,** PMO NF2648. Other material (paratypes): PMO NF2631, SM A109728–30.

NAME. 'Contradictory', referring to the unusual stipe form.

DESCRIPTION. This is a sufficiently distinctive species to warrant naming it on relatively little material. Even separate stipes are immediately recognizable. This is because the stipes, after their initial dorsal flexure, are curved in a fashion opposite to all other tetragraptids of which we are aware, being markedly convex along the dorsal side, so that the thecae are crowded together on the concave side. The degree of curvature varies: on the holotype it is marked near the proximal end and decreases distally, but on other specimens the stipe continues to curve

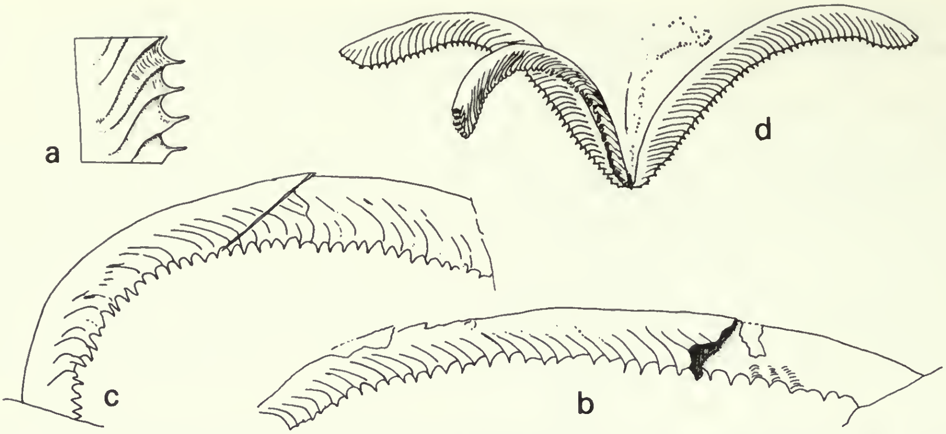


Fig. 31 *Tetragraptus contrarius* sp. nov. a, b, SM A109728, portion of stipe to show thecae (× 3) and full, gently curved, stipe (incomplete; × 2) respectively. c, A109729, well-preserved typically curved stipe; × 2. Both from Profilstranda, Olenidsletta Member, V$_2$a, 9 m above base. d, reconstruction of rhabdosome assuming moderate curvature of stipes; × 1.

fully through a quarter circle (Fig. 31c). Width of stipes is variable, ranging from 4 to almost 6 mm, and there is little change along the stipe, so that as in *T. serra* there is no taxonomic importance to be attached to thinner- or thicker-stiped variants. No proximal ends are well preserved, but it is possible to deduce that the initial thecae had low inclination, and that there was an abrupt narrowing of the stipes in the proximal region (? first two or three thecae of each stipe) much like the robust forms of *T. serra*. Some lengths of stipe in limestone are preserved in full relief, showing that the stipes had a rather narrow cross-section, about 0·8 mm across. Thecae initially with rather low (30°) inclination to dorsal wall, bending often abruptly near their apertures to become nearly normal to the dorsal wall. Apertures appear excavated deeply on flattened material, with long denticles forming a series of spines normal to the dorsal stipe margin. Well-preserved material shows that the thecal apertures are actually prolonged into spoon-like lips, 0·6 mm long or slightly more, the apertural margins being slightly concave (Fig. 31a). Distance between apertural lips is 1 mm or slightly less, resulting in a thecal spacing of 10–12 in 10 mm.

DISCUSSION. The distinctive habit of this species distinguishes it from all other *Tetragraptus* species. A few specimens described elsewhere, particularly *Tetragraptus denticulatus* of Hall (1865: pl. 4, fig. 13), show a gentle reflection like some of the less extreme stipes in our collection. Hall's species has narrower stipes (3 mm or less) and only about 8 thecae in 10 mm distally. Flattened material from New Zealand attributed to *T. headi* (J. Hall) by Cooper (1979: pl. 9, fig. c) shows a curious twist in the stipes near the proximal end; distal to this a stipe profile is presented, which is slightly convex in the manner of our species, but no apertures are visible in the proximal part. Such an appearance might result from plan-view flattening of species with *T. contrarius* morphology. If the proximal part were strongly recurved as in our species flattening may present us with a near-dorsal view of the stipes with no apertures visible; distally the stipes would have to bend to present a profile. In other features the New Zealand material compares with the narrowest of our specimens; it is from a younger horizon (zone of *I. victoriae maximodivergens*).

***Tetragraptus* cf. *hsui* Ge 1964**
Fig. 32

cf. 1964 *Tetragraptus hsui* Ge: 385–386, 399–400, text-figs 5a–b; pl. 3, figs 1–4.

STRATIGRAPHIC RANGE. Olenidsletta Member, 20–21 m above base, V$_1$b.

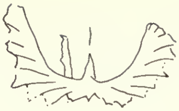


Fig. 32 *Tetragraptus* cf. *hsui* Ge. PMO NF2389, Olenidsletta Member, V_1a, 20–21 m above base, southern section; × 4.

MATERIAL. PMO NF2389.

DESCRIPTION AND DISCUSSION. Very small reclined tetragraptid. Sicula 1·7 mm long, first-order stipes probably of one theca each. Details of proximal development and structure unknown. Second-order stipes reach 1·4 mm wide by the level of their third theca and are only about 4 mm long. Thecae are relatively straight; measurements of their spacing are rather meaningless in such a small form.

Although not well preserved, the tiny size of the Spitsbergen form is distinctive and the general similarity of its rhabdosome, and thecal, form to Ge's figures of *T. hsui* (Ge 1964: text-figs 5a, b) from the Ningkuo Shale is striking. However, the Chinese form is associated with *Cardiograptus* and comes from a higher horizon (approximately latest Arenig). In view of this, and the paucity of the Spitsbergen material, we list the Spitsbergen form as *T.* cf. *hsui*.

Tetragraptus kindlei Ruedemann 1947
Fig. 33

1947 *Tetragraptus kindlei* Ruedemann: 306; pl. 50, figs 6–11.
1964 *Tetragraptus harti* Ge: 393; pl. 1, fig. 14; text-fig. 2.
?1973 *Tetragraptus kindlei* Ruedemann; Bouček: 23–25; pl. 1, figs 5–7; text-fig. 4a–d.
?1976 *Tetragraptus pogonipensis* Braithwaite: 30–31; pl. 8, figs 15–17, 19–21; pl. 14, figs 1–7.

STRATIGRAPHIC HORIZON. Olenidsletta Member, 20–21 m above base, V_1b.

MATERIAL. PMO NF2386.

DESCRIPTION AND DISCUSSION. The apex of the sicula is broken away, the apertural position projects slightly below the ventral margin of the 'funicle'. The first-order stipes together reach 3 mm in length and are comprised of a single, long, slender theca each. They appear to be slightly dependent. The second-order stipes are gently curved, becoming straight distally and were probably gently reclined in the original rhabdosome. The free walls of ventral thecae are inclined at a low angle (20°–30°).

The Spitsbergen specimen matches Ruedemann's description and illustrations well. *T. kindlei* was described from the *G. dentatus* Zone of the Glenogle Shale, British Columbia. The long, narrow initial thecae resemble those of species here referred to Subfamily Sigmagraptinae, but without the complete sicula this cannot be confirmed. The specimen from the Ningkuo Shale figured by Ge (1964: pl. 1, fig. 14) as *Tetragraptus harti* closely matches the Spitsbergen form.

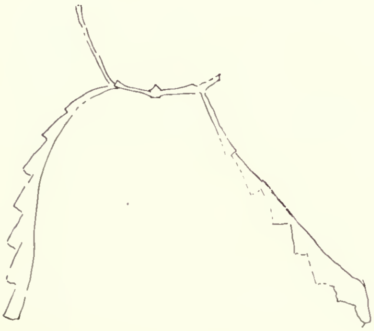


Fig. 33 *Tetragraptus kindlei* Ruedemann. PMO NF2386, incomplete mature rhabdosome. Olenidsletta Member, V_1b, 20–21 m; × 4.

The specimens from the Arenig of Bohemia described by Bouček as *T. kindlei* have a relatively long, narrow sicula and clearly isograptid development type. However, they have slightly closer thecal spacing (10 in 10 mm) and less curved second-order stipes, which appear to have been slightly declined or horizontal rather than reclined. They are therefore only tentatively included in the species here. *Tetragraptus pogonipensis* Braithwaite (1976: pl. 8, figs 15–17, 19–21; pl. 14, figs 1–7), from the Wahwah Limestone (mid Arenig), appears to have a similar overall rhabdosome morphology and a development type described as isograptid. However, its initial thecae are shorter and stouter than those of specimens here referred to *T. kindlei*, producing a shorter and broader 'funicle'.

Tetragraptus quadribrachiatus (Hall 1858)

Pl. 4, figs 13, 14

1858 *Graptolithus quadribrachiatus* J. Hall: 125.
1865 *Graptolithus quadribrachiatus* Hall; J. Hall: 91–92; pl. 5, figs 1–5; pl. 6, figs 5, 6.
1902 *Tetragraptus quadribrachiatus* (Hall) Elles & Wood: 57–58; pl. 1a–e.
1979 *Tetragraptus quadribrachiatus* (Hall); Mu *et al.*: 52; pl. 16, figs 6–9.
1979 *Tetragraptus quadribrachiatus* (Hall); Cooper: 66; pls 56, 96.

STRATIGRAPHIC HORIZON. 8·8–15 m above base of Olenidsletta Member, V_1a.

MATERIAL. PMO NF3319–20 and a few fragmentary specimens.

DESCRIPTION AND DISCUSSION. First-order stipes together form a 'funicle' 2 mm long; they appear to be comprised of a single theca each. Second-order stipes expand gradually in width and are straight and arranged more or less at right angles to each other. Full dorsoventral stipe width unknown as only the dorsal aspect can be seen. Thecal details unknown.

Tetragraptus quadribrachiatus has been widely reported around the world and apparently has a long time range. However, it is poorly known and the name may well embrace forms belonging to more than one species. The Spitsbergen material conforms to Hall's description in gross rhabdosome morphology. Although not well preserved, the first-order stipes appear to comprise a single theca each, as in most other tetragraptids. Ruedemann's (1947) claim that the first-order stipes of specimens from Deep Kill assigned by him to *T. quadribrachiatus* possess two thecae each would indicate that development of the rhabdosome did not follow the standard tetragraptid plan and his specimens may therefore not belong to Hall's species.

Other tetragraptids

A few Spitsbergen collections contain tetragraptids that are either too poorly preserved or too incomplete to allow definite identification.

Collections from the 125–130 m level (V_3) contain numerous fragments of stipes, up to 70 mm long, preserved in full relief. In only one specimen was the proximal region present allowing determination of the rhabdosome as that of a strongly reclined tetragraptid. Stipe width ranges from 2·9 to 3·4 mm and thecal spacing is 9–11 in 10 mm. The material possibly represents Ge's (1964) species *T. rigidus* but comparison is difficult owing to discrepancies between Ge's description and illustrations. For example, maximum stipe width is given as 4·3 mm (3·2 mm in one specimen) whereas, from his figured specimens, values of 3·0–3·5 mm seem more common. Similarly, thecal spacing is given as 7–8 in 10 mm (6 in 10 mm distally) whereas spacing measured off two of the figured specimens (one of which is the holotype) is 9–11 in 10 mm. Thus dimensions of the Spitsbergen specimens lie within the range of *T. rigidus* as determined from Ge's illustrations but differ somewhat from those given in his text. Because of this uncertainty, and the absence of information on the sicula and proximal structure of the rhabdosome, the Spitsbergen material is listed here as *T. rigidus*?

Genus ***DIDYMOGRAPTUS*** M'Coy, 1851

TYPE SPECIES. *Graptolithus murchisoni* Beck 1839.

CLASSIFICATION OF '*Didymograptus*'. Bouček (1973: 128–135) presented a general discussion of the principles of classification of dichograptoids in which he states several times that their 'generic differentiation . . . depends on their phylogenetic relationships' (p. 134). Such a putative view has been adopted, explicitly or implicitly, in a number of earlier accounts (Bouček & Přibyl 1951, Jaanusson 1960, Obut 1964). The old genus *Didymograptus* M'Coy has long been recognized as a form-genus which is likely to be polyphyletic (e.g. Nicholson & Marr 1895; Bulman 1936*a*), and in the last edition of the *Treatise* Bulman (1970: fig. 75) clearly indicates different phylogenetic routes by which graptoloids of *Didymograptus* grade might be derived.

This awareness of the polyphyletic nature of *Didymograptus* has led to the proposal of a number of genera purporting to be 'natural' groups of species. These include *Expansograptus* Bouček & Přibyl 1951, *Corymbograptus* Obut & Sobolevskaya 1964 and *Acrograptus* Tzaj 1969. These 'genera' formerly subsumed within *Didymograptus*, are based on gross rhabdosomal form; *Didymograptus*, *sensu stricto* constitutes the 'tuning-forks' with *D. murchisoni* as type species, *Expansograptus* includes extensiform species with *D. extensus* as type species, *Corymbograptus* deflexed forms with *D. v-fractus* as type species, and *Acrograptus* declined species with *D. affinis* as type species. These 'genera' are little more than upgraded versions of Elles & Wood's (1901) informal divisions. Bulman (1970) rejected these generic concepts, a rejection that Bouček (1973: 134) seems to interpret as a repudiation of the principle that dichograptid graptoloids ought to be classified phylogenetically. In practice what ought to be challenged is whether the characters taken as diagnosing the 'genera' are of any phylogenetic significance whatsoever. Curiously, Bouček (1973: 129–130) seems to reject proximal end development and structure as a criterion for classification in dichograptoids, and didymograptids in particular, on the presumption that because certain kinds of development were subject to natural selection, they were not of fundamental taxonomic importance. He goes on to show that *distal* characters, such as stipe width or thecal overlap, also vary in a species-to-species way, and were also therefore subject to low-level selection pressure. The basis for the presumption that gross rhabdosomal form is indicative of real phylogenetic links is not critically examined.

The material which can be isolated from the Arenig of Spitsbergen has cast new light on the importance of proximal structure in the classification of didymograptids. Complex proximal end characters indicate that truly phylogenetic classification not only splits up the old form-genus *Didymograptus*, but also cuts across the defined limits of the new, supposedly phylogenetic, genera. Bulman's caution in accepting *Expansograptus* and the like seems to have been fully justified. For example, we describe below a stratigraphic species lineage extending from '*Didymograptus*' *elongatus* to '*D.*' *formosus* in which a consistent and unusual proximal end structure is present (in this case the origin and growth of th1^1 on the antivirgellar side, when most contemporary graptoloids do not even have a virgella), while the gross rhabdosomal form changes from that supposedly characteristic of *Expansograptus* to that of *Acrograptus*. In this case the new 'genera' are unequivocally as much form-genera as was the old genus *Didymograptus*, and ones, moreover, without the partial justification of long historical usage. Within *Didymograptus*, *sensu stricto* (tuning-fork graptolites) there is evidence of a cluster of species of Arenig age in which the proximal end development is of isograptid type. The so-called *bifidus* stage ('dichograptid type') of development of Bulman (1936*a*) is based on Llanvirn material (wrongly attributed to *D. bifidus* Hall), where there is again a cluster of pendent species with similar development. Since the species from these different horizons are in almost all other respects perfect homeomorphs there is really no other recourse here but to regard the proximal end development as of fundamental phylogenetic importance.

As so often the case with graptoloids, the great majority of described didymograptids are known from flattened and imperfect type material. The form-genera at least permit a classification of these forms more finely than simply lumping them all as *Didymograptus*, but the point of so doing, if this does not reflect a phylogenetic grouping, is obscure: as they have similar ranges no stratigraphic purpose is served. However, there *is* a need to divide *Didymograptus* into monophyletic groups of species.

What we propose here is essentially a compromise. The form-genus *Didymograptus* is retained, specifically for those species of which proximal details cannot be determined. Monophyletic divisions of the genus are for the moment accorded subgeneric status. The names *Acrograptus, Corymbograptus* etc. are validly proposed, but they will have to be redefined in terms of the detailed structure of their type species before their use or otherwise in a phylogenetic classification can be assessed. The stipe attitude by itself is rejected as a basis for definition of groups.

Pendent didymograptids

The taxonomic state of the pendent didymograptids is in great confusion. The characters which have been generally employed are few; they are: 1, length of the sicula; 2, width of the stipes, and their rate of expansion from the proximal end; 3, thecal spacing; 4, acuteness of the thecal apertures; 5, divergence of the stipes; 6, thecal inclination. Not all these characters are independent of one another. Overall rhabdosome size has also been used, and larger size invariably accompanies thicker stipes with longer thecae (greater overlap) and higher distal thecal inclination. Most populations at any one horizon exhibit variation in these characters. It is bewildering to find that there has been a proliferation of new species names in the last few years (Braithwaite 1976, Bouček 1973, Mu *et al.* 1979); the last-named paper proposed 23 new species of pendent didymograptids without reference to the other two papers, in which seven new species were erected. Apart from the species proposed in the three papers listed above, pendent didymograptids include the following species (and this list is probably not exhaustive):

Didymograptus acutus Ekström 1937, *D. amplus* Elles & Wood 1901, *D. artus* Elles & Wood 1901, *D. bidens* Keble 1927, *D. bifidus* (Hall 1865) (and subspecies *latus* Ruedemann 1947), *D. bigcanyonensis* Decker 1944, *D. canadensis* Ruedemann 1947, *D. chapmani* Decker 1944, *D. chrbinensis* Bouček 1973, *D. clavulus* Perner 1895, *D. columbianus* Ruedemann 1947, *D. denticulatus* Berry 1960, *D. filiformis* Tullberg 1880, *D. flagellifer* Törnquist 1901, *D. furcillatus* Lapworth 1875, *D. geminus* (Hisinger 1840) (and subspecies *latus* Ekström 1937), *D. halli* Bouček 1932, *D. incertus* Perner 1895, *D. indentus* Hall 1858, *D. liber* Monsen 1937, *D. mendicus* Keble & Harris 1934, *D. minutus* Törnquist 1879 (and subspecies *pygmaeus* Monsen 1937), *D. miserabilis* Bulman 1931, *D. murchisoni* (Beck 1839) (with several named 'varieties', e.g. by Ekström 1937), *D. nanus* Lapworth 1875, *D. pacificus* Ruedemann 1947, *D. pakrianus* Jaanusson 1960, *D. pandus* Bulman 1931, *D. paraindentus* Berry 1960, *D. pendulus* Harris & Keble 1932, *D. protoartus* Decker 1944, *D. protobifidus* Elles 1933 (and subspecies *praecursor* Monsen 1937), *D. protogeminus* Decker 1944, *D. protoindentus* Monsen 1937, *D. protomurchisoni* Decker 1944, *D. rozkowskae* Kozlowski 1954, *D. smithvillensis* Berry 1970, *D. spinulosus* Perner 1895, *D. stabilis* Elles & Wood 1901, *D. turneri* Decker 1944, and *D. vacillanoides* Perner 1895.

This makes a grand total of about seventy species or subspecies of pendent didymograptids. Given the few characters available, and the variation in populations, it is difficult to see how so many taxa can be justified; there has been little in the way of population studies on the group. Earlier ideas about increase in size and robustness of the rhabdosome during the Llanvirn must now be modified, because giant, *murchisoni*-like species now seem to be found at all the earlier horizons as well, for example, from the early (Mu *et al.* 1979) or the mid (Berry 1970) Arenig. Continued thecal and stipe growth is evidently a polyphyletic character, and may even prove to be of less than specific significance in some lineages.

There has been no previous attempt to divide this pendent series of species into smaller generic units; Bouček (1973) evidently considered the pendent habit defined a monophyletic group. The type of *Didymograptus, sensu stricto* is *D. murchisoni.* Some species of pendent *Didymograptus* from the Llanvirn have th1^1 dicalycal at the *artus* (= what Bulman called *bifidus,* p. 171) stage of development; *D. artus* Elles & Wood (Skwarko 1967), *D.* sp. nov. aff. *minutus* (Skevington 1965: 24) and *D. rozkowskae* Kozlowski 1954 all described from isolated material, where the evidence is unequivocal. Bouček (1973) cites further examples with th1^1 dicalycal, which are less convincing as they are known only from flattened material, and which include at least five Llanvirn species, and two *(D. minutus minutus* and *D. chrbinensis)* from

Arenig strata. These last are very slender species and our experience with *Sigmagraptus* (below) indicates that very well-preserved material is necessary to be certain of the development of such forms. In any case it is certain that there is a cluster of species from Llanvirn localities with th1^1 as the dicalycal theca. In these species th1^1 also originates low down on the sicula, well below the prosicula and often low on the metasicula.

The concept of *Didymograptus, sensu stricto* has perforce to be based on *D. murchisoni,* the type species. Unfortunately, the development of *Didymograptus murchisoni* is not known from isolated material. Bulman (1936*a*: 84) showed th1^1 dicalycal but in his accompanying text attributes the development to the *minutus* stage. Subsequently the *minutus* stage (Bulman 1970: 74) became a division of the isograptid type of development (i.e. with th1^2 dicalycal), but Bulman did not state whether he believed that *D. murchisoni* should now be regarded as having th1^2 dicalycal. Re-examination of the type series of *D. murchisoni* is not very helpful; all that can be said of the specimens, which have a little relief, is that *none* show the isograptid arch. To this we would add that British material termed *D. bifidus* (*non* Hall 1865) has th1^1 dicalycal, and *D. murchisoni* is clearly related to this form and may be no more than a stout variant of it. Another related species, *D. pakrianus* Jaanusson 1960, also probably has th1^1 dicalycal, and some specimens of *murchisoni* from Abereiddy Bay are extremely close to *pakrianus* itself. Taken together this evidence suggests that the type species of *Didymograptus* had a proximal end development like that of *D. artus* and Welsh material commonly (and incorrectly) termed *D. bifidus* has th1^1 dicalycal.

Well-preserved isolated specimens of what we believe to be the true *Didymograptus bifidus* (Hall) show a perfect isograptid development, with th1^2 dicalycal (Fig. 34a, b). In this case th1^1 has a high, possibly prosicular origin which has the effect of broadening the pyramid formed by the sicula + proximal thecae (sicula 'wedge') as seen in flattened material. Some of our pendent Arenig forms have this type of sicular 'wedge'. Braithwaite (1976) had previously remarked on isograptid development in flattened pendent *Didymograptus* from Utah. There thus appears to be a cluster of Arenig species with isograptid development.

It therefore seems reasonable to introduce a taxonomic distinction between the two main types of development. For those pendent didymograptids with isograptid development and an

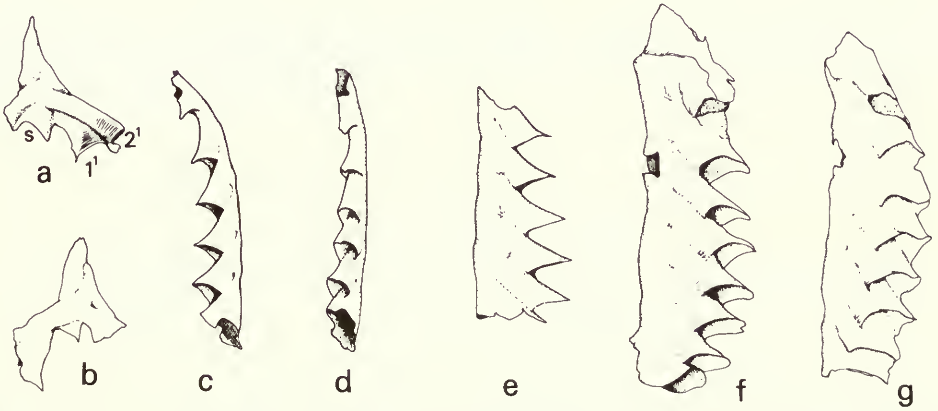


Fig. 34 *Didymograptus (Didymograptellus) bifidus* Hall. a, b, PMO NF3345, NF3346 respectively; × 16. Isolated proximal portions, reverse views: note isograptid arch and origin of th2^1 near proximal part of th1^2, proving the assignment to *Didymograptus (Didymograptellus).* c–g, isolated stipe fragments from same horizon as a and b to show change in thecal form along stipe; all × 8. c, d, NF728, proximal part of stipe from th1, two views. e, NF734, mid part of stipe. f, g, NF748, distal part of stipe showing transverse thecal apertures (specimen slightly crushed proximally); the right hand view shows how thecae may become imbricated during flattening. All 75 m from base of Olenidsletta Member on Profilstranda.

origin of th1[1] high on the sicula we introduce the new subgenus *Didymograptus (Didymograptellus)*. In contrast to Bouček (1973) we regard it as probable that *Didymograptus (Didymograptus)* and *Didymograptus (Didymograptellus)* are phylogenetic groups. The utility of this distinction is shown by the fact that the European specimens of what has been called *D. bifidus* (and gives its name to the zone) has *artus* development, whereas if we are correct in our determinations true *D. bifidus* is a *Didymograptellus* species. This would put to an end the excessively protracted debate about whether the North American and European zones of *D. bifidus* can be correlated on the basis of the eponymous species.

Subgenus ***DIDYMOGRAPTELLUS*** nov.

TYPE SPECIES. *Graptolithus bifidus* Hall 1865.

DIAGNOSIS. *Didymograptus* with pendent habit, rhabdosome gracile to robust. Theca 1^1 typically originates high on sicula, and of similar length to sicula. Theca 1^2 dicalycal, with normal isograptid development.

NAME. Diminutive of *Didymograptus*.

DISCUSSION. The proximal end development distinguishes *Didymograptellus* from *Didymograptus* in the restricted sense. This inevitably leaves many pendent species for which the proximal structure is not fully known, and for these the generic name *Didymograptus* has to be used *sensu lato*. It is now clear that the development of *Didymograptus (Didymograptus)* with th1[1] dicalycal is not primitive, but a derived condition with only a few known exemplars (Cooper & Fortey 1982). *D. (Didymograptellus) multiplex* sp. nov., described below, indicates a mechanism by which the *artus* type of development can be derived from the isograptid type. In flattened material there are obvious problems in distinguishing the two types of development. Where th1[1] grows down beside the sicula this broadens the cone at the apex of the flattened rhabdosome with angles of about 25°–30°; in *Didymograptus (Didymograptus)* species with low metasicular origin of th1[1] the sicula looks markedly acute, with an apical angle of about 10°–15°. Any tectonic distortion removes such discriminating characters.

Although the high sicular origin of th1[1] is typical of *D. bifidus* we also include in *Didymograptellus* those species, like *D. minutus* , which retain isograptid development, but apparently with a low sicular origin of th1[1].

INCLUDED SPECIES. *Didymograptus bifidus* (Hall 1865); *D. minutus* (Törnquist 1879), *D. fillmorensis* Braithwaite 1976 and *D. millardensis* Braithwaite 1976. Most of the forms identified in the past as *Didymograptus protobifidus* Elles 1933 probably belong here. The subgenus ranges from the North American subcontinent, through Spitsbergen to northeastern Russia, China, Australia and New Zealand. The *minutus* stage species are found in Scandinavia.

Didymograptus (Didymograptellus) bifidus (Hall 1865)

Figs 34a–g, 35f; Pl. 5, figs 11, 12

?*non* 1858 *Graptolithus bifidus* Hall: 130 (*nomen dubium;* ambiguous description, no figure).
1865 *Graptolithus bifidus* Hall *(pars)*: 73–74; pl. 1. figs 16–18; *non* pl. 3, figs 9, 10.
non 1870 *Didymograptus bifidus* (Hall) Nicholson: 346, fig. 7.
?*non* 1875 *Didymograptus bifidus* (Hall); Lapworth *in* Hopkinson & Lapworth: 646; pl. 33, fig. 8.
non 1901 *Didymograptus bifidus* (Hall); Elles & Wood: 42–44; pl. 4, fig. 1.
1904 *Didymograptus bifidus* (Hall); Ruedemann: 689–692; pl. 15, figs 1–3.
non 1931 *Didymograptus* aff. *bifidus* (Hall); Bulman: 33, fig. 10; pl. 12, figs 6, 7.
non 1937 *Didymograptus bifidus* (Hall); Ekström: 26, pl. 2, figs 9–14.
1944 *Didymograptus bifidus* (Hall); Decker *(pars):* 382, figs 31, 32; ?*non* figs 29, 30.
? 1944 *Didymograptus protoartus* Decker: 384, fig. 4.
1947 *Didymograptus bifidus* (Hall); Ruedemann: 327–328; pl. 54, figs 11–16.
1947 *Didymograptus columbianus* Ruedemann: 329; pl. 54, figs 25–29.
non 1950 *Didymograptus bifidus* (Hall); Phillipot: 241.
1960 *Didymograptus bifidus* (Hall); Berry: 59; pl. 10, figs 3, 7–10.

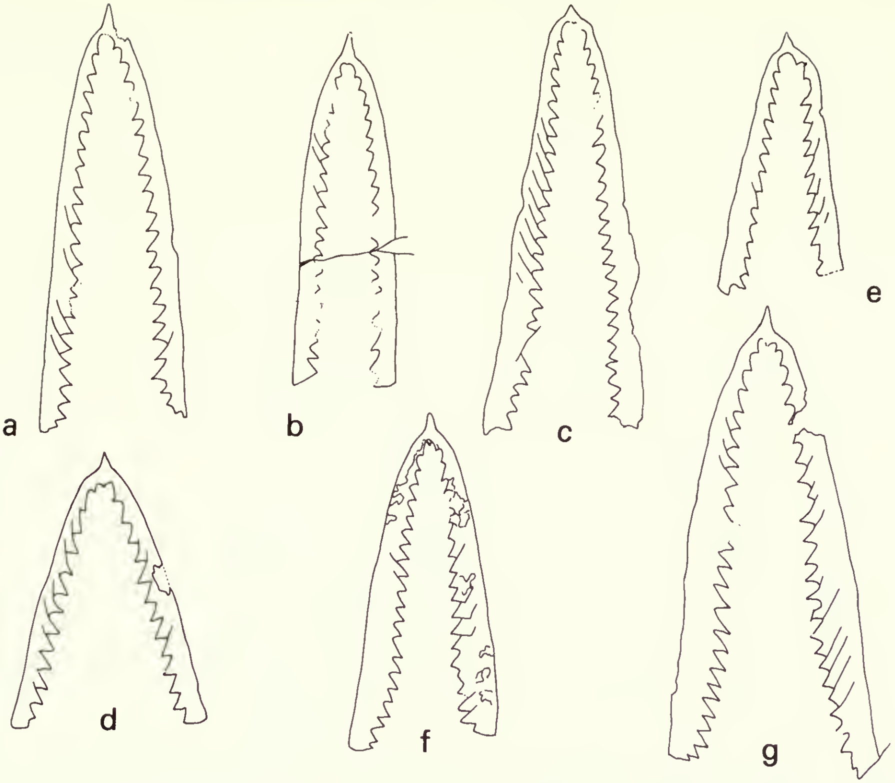


Fig. 35 Flattened didymograptids of the *Didymograptus (Didymograptellus) bifidus – 'protobifidus'* morphological group. a–d, *D. (D.) 'protobifidus'* Elles. a, SM A105812, typical example, close to holotype; type section, 57 m from base of Olenidsletta Member. b, holotype, Skiddaw Slates, English Lake District, BM(NH) Q7. c, PMO NF657, large example transitional in morphology with *D. (D.) bifidus*; about 70 m from base of Olenidsletta Member on Olenidsletta. d, NF824, specimen with stipes splayed more widely than usual, 35 m from base of Olenidsletta Member on Profilstranda. e, *D. (D)* cf. *meitanensis* Chen, NF2849, 17 m from base of Olenidsletta Member, Profilstranda. f, *D. (D.) bifidus* Hall, specimen GSC 56912 from Hall's type population, close to the specimen of Fortey (1976: text-fig. 3b). g, *D. (D.) diapason* Chen & Xia, NF834, 35 m from base of Olenidsletta Member. All × 3.

1960 *Didymograptus bifidus* (Hall); Thomas: 17 (older Australian records are *D. protobifidus, fide* p. 27).
1962 *Didymograptus bifidus* (Hall); Berry: 294–297, text-fig. 1a–d.
1970 *Didymograptus bifidus* (Hall); Berry: 64, figs 1b, c, f, 2c.
non 1973 *Didymograptus* cf. *bifidus* (J. Hall 1865); Bouček: 98–101; pl. 15, fig. 8; text-fig. 31.
1976 *Didymograptus bifidus* (J. Hall); Fortey: 274–275, text-fig. 3.
? 1979 *Didymograptus bifidus* (Hall); Mu *et al.*: 70; pl. 23, figs 11–15.

STRATIGRAPHIC RANGE. 75 m to 93 m from base of Olenidsletta Member on type section; sporadic through V_2 on Olenidsletta outcrops; total range from V_1c to V_2a (Arenig; *D. bifidus* Zone).

MATERIAL. Specimens additional to those given in Fortey (1976: 274) include isolated proximal ends PMO NF3345–6, distal isolated stipes NF728, NF734, NF748, relief specimens on rock NF621 and NF2031 (slender form).

DESCRIPTION. This species has already been discussed by Fortey (1976), who showed that specimens from Spitsbergen could be matched with those from the Marathon region, Texas, which form the basis of the zone of *D. bifidus* in North America. We have now succeeded in isolating some relief material, which merits further description. Isolated proximal ends are mostly of mature specimens, thickened with secondary periderm. The sicula is 1·0–1·2 mm long, measured from the base of the very short nema, which does not exceed 0·2 mm in length. The aperture of the sicula is extended on the ventral side into a short, rounded lip about 0·2 mm long. The sicular aperture is oval, its long axis in the median plane of the rhabdosome being 0·30–0·35 mm long, the shorter axis about two-thirds of this. Theca 1^1 originates within 0·2 mm of the top of the sicula, and is closely similar to the sicula in shape and dimensions, its long axis making an angle of about 30°–35° with that of the sicula, and its free ventral wall extending at least 0·4 mm away from the lower part of the sicula. The divergence of the sicula and th1^1 occurs about 0·2 mm above the base of the sicula on its ventral side. Budding of th1^2 is near the top of th1^1, and its downward growth across the sicula to form the second stipe is such as to make an approximate right angle with th1^1. Total length of th1^2 is about 1·3 mm. Theca 2^1 originates within 0·2–0·4 mm of the top of th1^2, forming an obtuse angle with it as it curves over the back of th1^1 to form the second stipe. Proximal width of th2^1 is about 0·2 mm. The arch formed by the ventral walls of the proximal parts of thecae 1^2 and 2^1 in reverse aspect is a conspicuous feature of the relief material, but since it passes above the embayment between the sicula and th1^1 it would not necessarily be seen on severely flattened material. Theca 1^2 is dicalycal and the distance between the proximal parts of th2^1 and th2^2 is about 0·6 mm, so that the two daughter thecae are well separated. Proximal thecal apertures are, like the sicular aperture, elongate oval in the dorsoventral (sagittal) plane. In the population from which the isolated material has been obtained the stipes widen rather rapidly, and as the thecae increase in length so the apertures become progressively more transverse, finally becoming transversely elliptical at about th20. The distal stipe fragments are very robust, the transverse width being 1·1 mm where the dorsoventral stipe width is 1·9 mm. The distal thecal apertures are strongly excavated, the apertural margin making an angle of 30°–40° with the ventral wall of the theca. The mid-part of the apertural margin is prolonged into a short lip, which appears in flattened material as a tiny denticle. Note that the interthecal septa are slightly shorter than the free dorsal wall on distal material, and may be slightly curved; at their inner ends they make distinct dimples in the exterior rhabdosome wall. Isolated distal fragments have about 16 thecae in 10 mm, and we have observed little change in thecal spacing along the stipes.

Comparative remarks. The isolated material comes from a horizon 75 m from the base of the Olenidsletta Member, low in the range of the species. As noted by Fortey (1976), the early population here tends to have stipes that diverge at up to 30°, a higher angle than that noted by Berry (1962) in his description of the four specimens of *Didymograptus bifidus* from the type locality. However, there are specimens from only a little higher in Spitsbergen which have distal stipe divergence as low or lower than type *D. bifidus* (Pl. 5, fig. 11), and this character is so variable that no importance is here attached to it. Hall's types are not well enough preserved to show development but they clearly show the short 'paired' structure of sicula and th1^1 that typifies our isolated material. There is a complete transition between *Didymograptus (Didymograptellus) bifidus* and *D. (Didymograptellus) 'protobifidus'* which underlies it in the Olenidsletta Member (Figs 36, 37), but the earlier species merits taxonomic recognition because it is clear that there is a change at the population level between the two, and one which is of stratigraphical importance. The simplest difference to use is the distal thecal spacing, 12–13 in 10 mm in the typical *'protobifidus'* populations and 14–16 in 10 mm in typical *bifidus* populations. Closer thecal spacing pertains even in individual specimens of *D. bifidus* which are otherwise more like *D. 'protobifidus'* in stipe attitude and thecal expansion rate. Fig. 37 shows the gradients obtained from the straight line fits on the stipe expansion diagram, which shows a shift in the populations as a whole towards higher gradients (= greater increase in width of stipe per theca) from *'protobifidus'* to *bifidus*. It is obvious that there is stratigraphical overlap between populations of the two species, and specimens with thecal spacing 13–14 in 10 mm distally and with stipe expansion gradient of about 1·5 should best be referred to as *'protobifidus'–bifidus* transitions. Hall's type populations and others from Quebec seem to

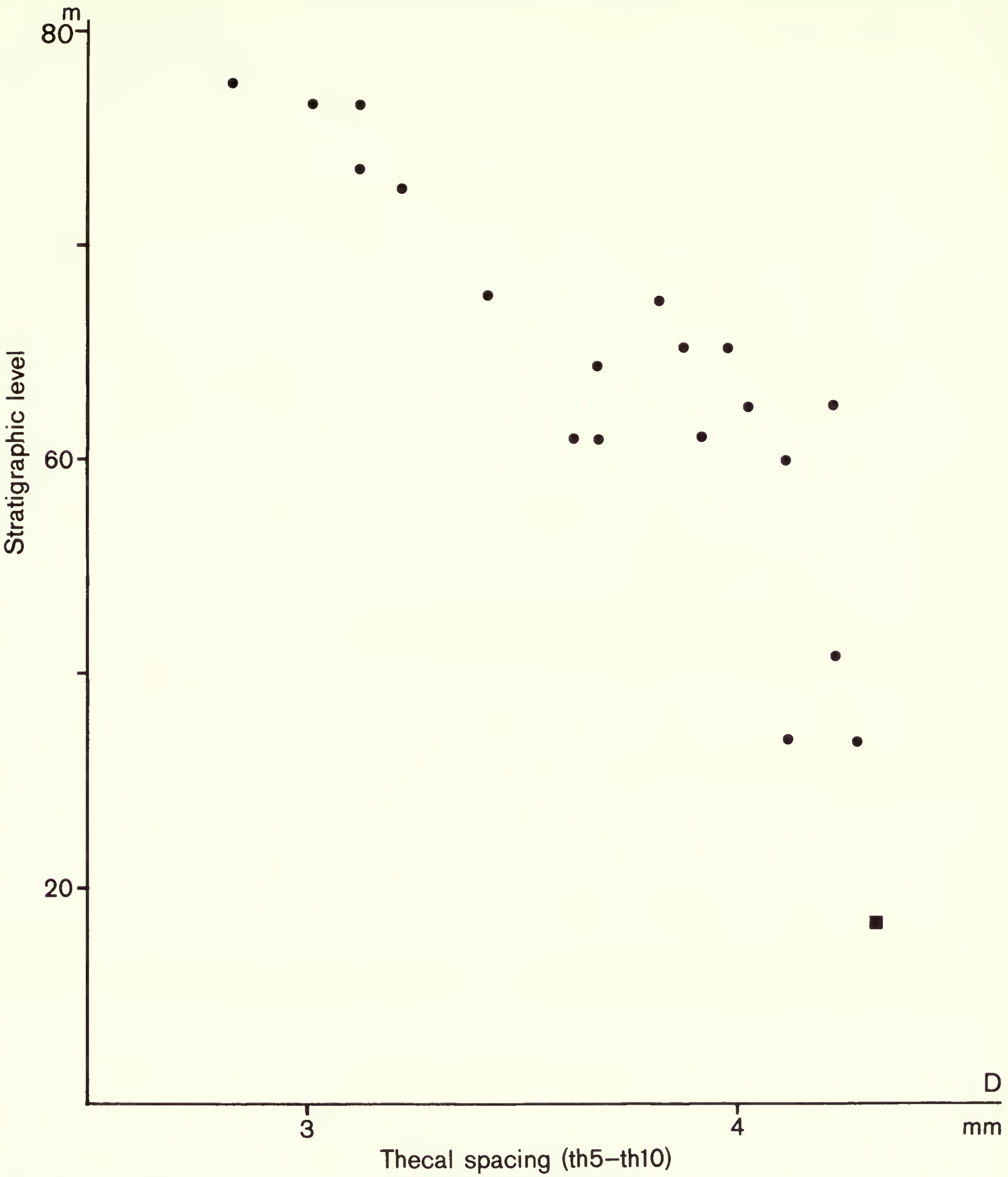


Fig. 36 *Didymograptus (Didymograptellus) 'protobifidus'* to *D. (D.) bifidus* series, plot of thecal spacing against stratigraphic occurrence in metres from base of Olenidsletta Member. Spacing is taken as distance from the apertural denticle of th5 to that of th10 as standard. Square at 17 m is for *D. (D.)* cf. *meitanensis* Chen.

include forms which are like typical Spitsbergen *bifidus* as well as some that may be *'protobifidus'–bifidus* transitions: in other words the type population may be from a horizon low in terms of the range of *D. bifidus* in Spitsbergen. Hall's population occurs along with other extensiform didymograptids and phyllograptids which prove its Arenig age. Since *D. 'protobifidus'* has distal thecae with the apertures less deeply excavated than those of *D. bifidus,* so that the angle of the apertural margin to the ventral wall of the theca is 45°–50°, it is expected

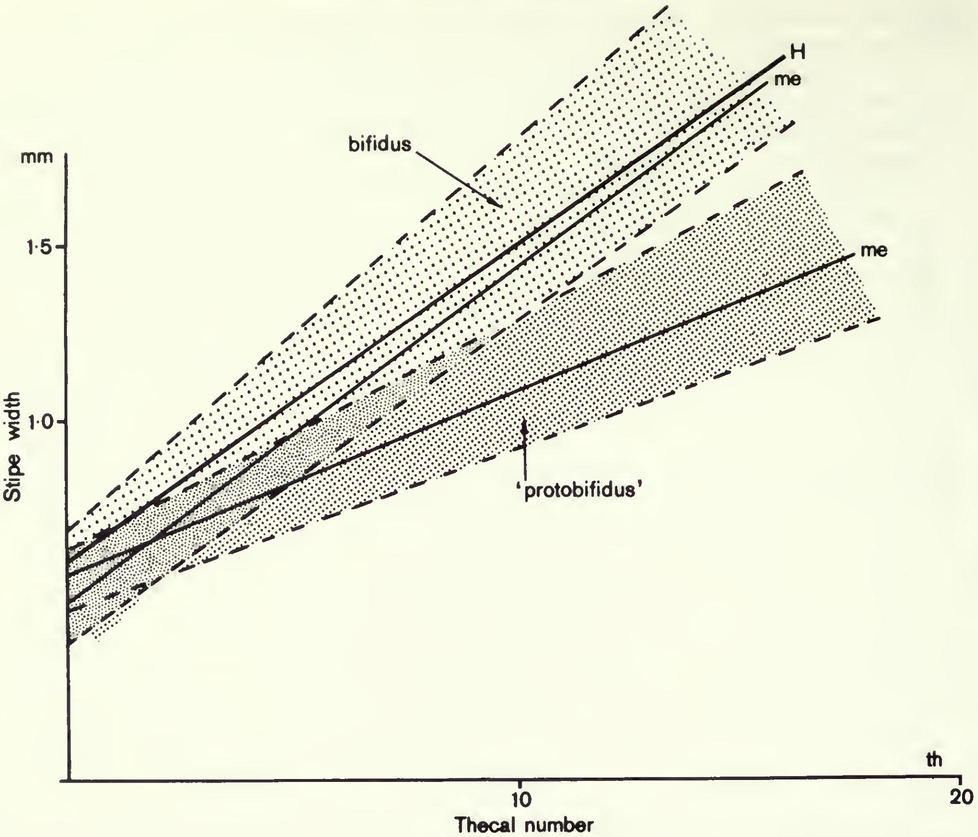


Fig. 37 Stipe expansion diagram for the populations *Didymograptus (Didymograptellus) 'protobifidus'* to *bifidus*. Spread of calculated regressions for the populations of these two stratigraphically intergrading species from the Valhallfonna Formation. Dense stippling shows *'protobifidus'*; light stippling shows *bifidus*; me – median regression line for both species. H is the regression for the specimen of *D. bifidus* from Hall's type population illustrated in Fig. 35f.

that the distal thecae of *D. 'protobifidus'*, when eventually found in relief, will be found to retain more of the character of the proximal thecae they more closely resemble, i.e. elongate rather than transverse apertures.

The British material that has been referred to *D. bifidus* has th1^1 dicalycal rather than th1^2, and is therefore not conspecific, but distal thecal and stipe characters are very similar to those of *D. bifidus, sensu stricto.* Another difference is that the British material, when well-preserved, shows a long, narrow and gently tapering sicula, for which lengths of 1·5–2·0 mm are common. Unlike North American *D. bifidus* the nema is not clearly differentiated from the sicula. The low origin of th1^1 can also be seen on some British specimens having partial relief, but this detail is obscured when the specimens are preserved as a white film, as at Abereiddy Bay. Obviously, a different name has to be applied to the British specimens, of which *D. spinulosus* Perner 1895 may be the senior.

A welter of pendent *Didymograptus* species have been described from China by Mu *et al.* (1979). In south-west China a zone of *D. deflexus* (which is not the time equivalent of the zone of the same name in Britain as shown on their p. 11) is divided into several subzones, partly on the basis of pendent didymograptids. The occurrence in this same interval of true *Phyllograptus* (as restricted in this paper – p. 273) is good evidence of its contemporaneity with the *'protobifidus'–bifidus* interval in Spitsbergen. Most of thse species seem to have been based on a holotype-to-holotype comparison with previously described species, and preservation is not adequate to determine proximal end structure. The species identified as *D. bifidus* apparently occurs stratigraphically *underneath* a species identified with *D. protobifidus* in south-west China; if we are correct in deducing a continuous transition from *D. 'protobifidus'* to *D. bifidus* in Spitsbergen, one or other of the determinations from China must be incorrect. Many of the other species supposedly endemic to south-west China – *D. eobifidus, D. subtilis, D.* cf. *protoartus, D. meitanensis* and *D. wudangensis,* for example – may prove to fall into the range of variation shown in the series *'protobifidus'* to *bifidus,* and without further information on the intraspecific variation in the populations of pendent species from south-west China the taxonomic status of these species must be viewed with caution. But it is important to note that the Chinese pendent didymograptids are divided into two groups stratigraphically, one Arenig and the other Llanvirn, separated by a gap. The earlier of the two may be those with isograptid proximal end development, the later with th1^1 dicalycal.

Braithwaite (1976) has a similar gap in Utah between pendent species of Arenig age and one of probable Llanvirn age. However, he has determined the latter as *D. bifidus*, which is puzzling, now that European Llanvirn *bifidus*-like forms have been shown to belong to a different species on the basis of their proximal end development. The sicula attributed to the species by Braithwaite (1976: pl. 16, fig. 2) cannot belong to it, as it clearly shows the long virgella characteristic of the Phyllograptidae. Braithwaite states that the *D. bifidus* from Utah has isograptid development, but this cannot be clearly seen from the figured specimen. The origin of th1^1 appears lower on the sicula (1976: pl. 16, fig. 4) than is the case in our *D. bifidus* and the prosicula is extended into a tube. These differences may be enough to suggest that the Utah form is a different species.

D. bifidus in the restricted sense (with the possible exception of the Utah specimens) seems to be confined to Arenig rocks of the Pacific province, corresponding broadly with the Ordovician equatorial regions: Texas (Berry 1960), Quebec, Newfoundland, Spitsbergen, south China and the Canning Basin, Western Australia furnish specimens which can be definitely assigned. Oddly enough, in what might be termed the classic 'black shale' graptolite facies (Australia, New Zealand, western Ireland, Yukon, and western facies in the Basin Ranges of Idaho) it appears to be lacking, although *'protobifidus'* is present. It seems that there may have been some facies control on its appearance, and it may prove to be confined to the more inshore of Arenig successions.

Didymograptus (Didymograptellus) diapason Chen & Xia *in* Mu *et al.* 1979
Fig. 35g

1979 *Didymograptus diapason* Chen & Xia *in* Mu *et al.*: 68; pl. 22, figs 7–15.

STRATIGRAPHIC RANGE. Olenidsletta Member, V_1b, 35 m from base in type section, middle Arenig (*D. protobifidus* Zone).

MATERIAL. PMO NF824, NF834.

DESCRIPTION. The name *Didymograptellus diapason* is applied to a small population of stout 'tuning-forks' from low in the Olenidsletta Member, which are essentially similar to *D. 'protobifidus'*, but in which the stipes distally attain a much greater thickness. The sicular 'wedge' shows the broad cone characteristic of the *bifidus–'protobifidus'* group as a whole (length 1·3–1·5 mm) and presumably consists of the sicula and th1^1 growing downwards together. The proximal two or three thecae on each stipe are similar to *D. 'protobifidus',* but thereafter the stipes thicken up to a marked degree, so that on the stipe expansion diagram (Fig. 38) the gradients are much steeper than in that species. Our specimens do not reach the length of some of the Chinese type population, but the rate of stipe expansion is identical to that given by Chen & Xia (*in* Mu 1979: 68), such that at th15 the width is 2·1 mm. Thecal inclination (so far as it is visible on our rather poor material) remains constant at about 40°, even when the stipes become quite thick. The free dorsal wall of the thecae at th5 is 0·8–1 mm long and remains almost constant thereafter. Apertures are deeply excavated with a small to moderate acute angle between dorsal and apertural margins in profile. Most important, thecal spacing is low for a pendent species, remaining at 12 or 13 per 10 mm distally, the same as that in *D. 'protobifidus'*.

Discussion. This species is probably a *D. 'protobifidus'* derivative in which thecal growth has continued in the distal part of the stipe. Similar thick species appear to have been derived on several occasions within the pendent didymograptid group. Of these only *D. diapason* has such low thecal spacing distally, and the thecae do not appear to become curved as width increases.

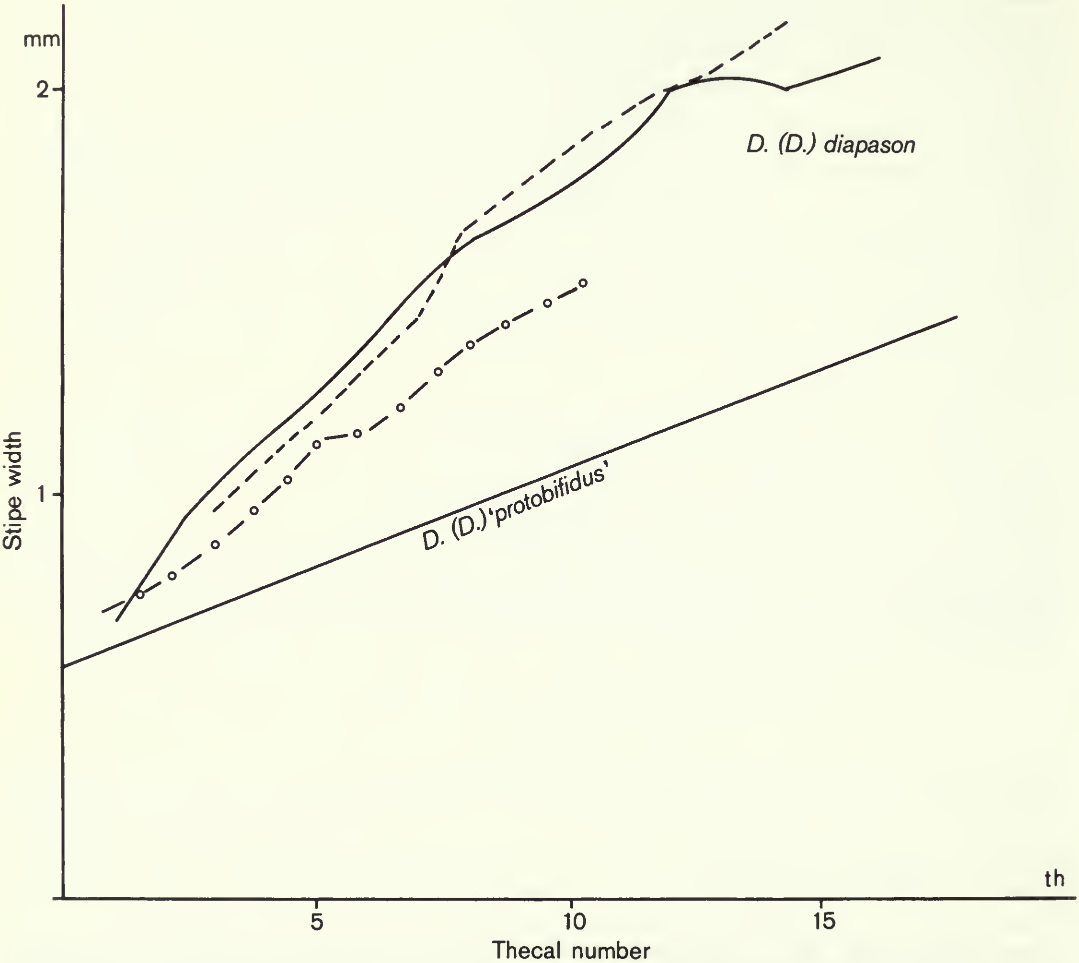


Fig. 38 Stipe expansion diagram for *Didymograptus (Didymograptellus) diapason* Chen & Xia. Median regression for *D. (D.) 'protobifidus'* shown for comparison.

Of other Arenig species with thick stipes *D. millardensis* Braithwaite (1976: 43–44; pl. 9, figs 24–26) has densely spaced thecae, as does its probable senior synonym *D. smithvillensis* Berry (1970: 67, 69; figs 1e, g, 2a, b); both are likely to be 'overgrown' forms of *D. bifidus, sensu stricto,* and as such slightly younger. The taxonomic recognition of these stout forms is probably justified as they seem to form discrete populations. However, it is now clear that broad, *murchisoni*-like species existed in the earlier part of the middle Arenig as well as in the Llanvirn.

Didymograptus (Didymograptellus) cf. **exilis** Ni *in* Mu *et al.* 1979

Fig. 39a–c; Pl. 5, figs 4, 5

cf. 1979 *Didymograptus exilis* Ni *in* Mu *et al.*: 58; pl. 19, figs 11, 12.

Stratigraphic range. From one bed in the Olenidsletta Member, 49 m from base, V_1b, *D. protobifidus* Zone, associated with *Isograptus scandens* sp. nov. (p. 257).

Material. PMO NF3381–4, and several others.

Description. This small species lies outside the *bifidus–'protobifidus'* group to which the two species above belong. Isograptid development is interpreted from one specimen (Fig. 39b); this seems to be associated with the slightly lop-sided appearance of the proximal end, the squarer side being where the crossing canal comes over the back of th1^1 to initiate the second stipe. Hence we assign the species to the subgenus *Didymograptellus*. Sicula is 1·1 mm long, including a short nema 0·1 mm long, and its distal width is about 0·25 mm where it is prolonged into a lip forming a distinct, acute projection. Theca 1^1 originates very high on the sicula, almost certainly from the prosicula, attaining a length of 1·4 mm. Acute angles between the dorsal wall and apertural margins are typical of this, and all subsequent thecae. Theca 1^2 of similar character, but with its aperture about 1 mm along the opposing stipe. Maximum stipe curvature is at these first two thecae so that by the second thecal apertures on both stipes the stipes are virtually parallel and remain so thereafter. At the level of the first theca stipe width (dorsal margin to tip of thecal denticle) is only 0·5 mm. Stipe width increases slowly and slightly to a maximum of about 0·8 mm at th3, and is virtually constant thereafter to th8 (beyond which our specimens do not grow). Thecal inclination is constantly low (20°–25°), with corresponding low thecal overlap. Distance between apertural denticles on proximal thecae is large (about 0·75 mm), and the spacing becomes closer distally, down to as little as 0·5 mm, but the specimens are too small for spacing in 10 mm to be meaningful.

Discussion. This species, with its slender stipes, low thecal inclination and small size is clearly different from the *'protobifidus'* populations which are the commoner pendent populations at this horizon. While its general habit recalls such species as *D. nanus* Lapworth 1875, the sicula in that species is long and narrow (exceeding 2 mm in length) and th1^1 has an origin low on the metasicula, and as such is typical of the Llanvirn group of species for which the development is typified by *D. minutus*. It is unlikely to be closely related.

Ni (*in* Mu *et al.* 1979: 58; pl. 19, figs 11, 12) described the slender species *D. exilis* from a similar horizon to the Spitsbergen form in south-west China; like our species it shows conspicuous asymmetry at the proximal end, and is similar with regard to length of sicula and thecal

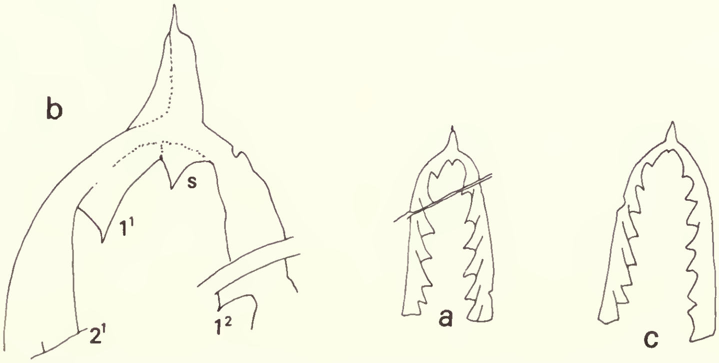


Fig. 39 *Didymograptus (Didymograptellus)* cf. *exilis* Ni. a, b, PMO NF3343, rhabdosome (× 3) and enlargement of proximal end (× 12), showing indication of isograptid arch, accounting for lop-sided appearance of flattened profile, and demonstrating *Didymograptellus* affinity. c, NF3344; × 3. Both 50 m from base of Olenidsletta Member on Olenidsletta, in bed with *Isograptus scandens* sp. nov.

inclination. Ni's specimens are smaller, not growing beyond th3 or 4, and if anything the stipes are even narrower. Ni also mentions a supposed *artus* development in her text; as we have shown elsewhere, development types are especially difficult to discern on slender species without isolated material, and particularly in view of the similar asymmetrical appearance of *D. exilis* to our material, we consider it possible that the Chinese material may also have had isograptid development. However, we are bound to record our caution in identifying with the Chinese species, and the determination is accordingly tentative.

Monsen (1937) has described several slender *Didymograptus* species from the Arenig of Norway: *D. protoindentus* Monsen, *D. nanus* Lapworth, *D. minutus* Törnquist and a subspecies *pygmaeus* Monsen, and *D. protobifidus praecursor* Monsen. Of these the first and last named have stipes that diverge distally and have long siculae, exceeding 2 mm in length. The type specimen of *D. minutus* Törnquist (1890: pl. 1, figs 7, 8; see Bouček 1973: 78) is also from Arenig strata in Sweden, but unlike our species the sicula carries a long nema, and even without it is about 2 mm long. Monsen's subspecies *pygmaeus* is not well described, but if the stipe width quoted (0·3 mm) is correct this is far narrower than our material. The specimens attributed to *D. nanus* by Monsen differ from the Llanvirn type examples of that species in the same way as our material, mentioned above. Monsen (1937: pl. 2, fig. 38) clearly indicates a high sicular origin for th1^1, and her pl. 2, fig. 39 shows the arch formed by the crossing canals as typically seen in the isograptid development (see *D. bifidus* herein). Hence these *'nanus'* specimens are very like our specimens from Spitsbergen here attributed to *D.* cf. *exilis*; the sicula appears to be slightly more acute on Monsen's figures. Obviously it would be desirable to have more information on population variability in this case, and there are not enough specimens from Spitsbergen to provide it. But the probability is that the Chinese, Norwegian and Olenidsletta Member specimens belong to a single species.

Didymograptus (Didymograptellus) cf. ***meitanensis*** Chen *in* Mu *et al.* 1979
Fig. 35e

cf. 1979 *Didymograptus meitanensis* Chen *in* Mu *et al.*: 61; pl. 20, figs 7–9.

STRATIGRAPHIC RANGE. The earliest pendent didymograptid in the Spitsbergen succession, 17 m from base of the Olenidsletta Member, Lower Arenig (high Bendigonian).

MATERIAL. PMO NF2844, NF2849.

DISCUSSION. This early pendent species is similar to *D. 'protobifidus'* in most respects, but occurs stratigraphically below the abundant typical forms of that species, such as those shown on Pl. 2, fig. 1, and with a late Bendigonian fauna having *Tetragraptus (Pendeograptus) fruticosus* as a common associated species. This didymograptid has the lop-sided appearance of the proximal end that we associate with *Didymograptus (Didymograptellus)*. Like *D. 'protobifidus'* the thecal spacing is only 12–13 in 10 mm; stipes achieve a maximum width of about 1·3 mm. The main difference from *D. 'protobifidus'* resides in the higher degree of thecal overlap, so that the stipes lack the deeply indented appearance characteristic of *D. 'protobifidus'*. At about th10 *D. 'protobifidus'* typically has the thecal aperture cutting in to nearly half the total stipe width, whereas in *D.* cf. *meitanensis* that is only about a third. This may well represent the earliest stage of the *'protobifidus'–bifidus* population shift, but because of its early stratigraphic occurrence the form is recorded separately here. Mu *et al.* (1979) have named a large number of pendent species from about the same horizon as our species, but it is difficult to use the descriptions of the Chinese material for a critical determination of our specimens. *D. eobifidus* Chen & Xia (*in* Mu *et al.* 1979: 60–61; pl. 20, figs 1–6) is generally similar, but the quoted thecal spacing is denser (about 15 in 10 mm measured from their photographs). The closest species from the Chinese descriptions is probably *D. meitanensis* Chen, and we tentatively compare our material with that species. What is clear is that the Arenig pendent didymograptid radiation has produced a highly variable set of morphotypes (matching that in the Llanvirn); how many of these are 'real' species will depend on careful numerical analysis, and especially on the discovery of more material which can be isolated.

Didymograptus (Didymograptellus) multiplex sp. nov.

Pl. 1, figs 1–5

DIAGNOSIS. *Didymograptellus* species showing a transition from isograptid to *artus* development. Theca 2^1 typically aborted, not giving rise to a stipe series. Theca 1^1 dicalycal, development dextral. Habit slender, sicula about 1 mm long; stipe width at first theca only 0·5 mm, about 1·1 mm at sixth theca. Thecae with very low inclination, apertures deeply indented, flared, with prominent denticles.

STRATIGRAPHIC RANGE. High mid-part of the Olenidsletta Member (V_2a), the youngest pendent didymograptid in our section. 91 m from base, upper part of the Arenig *D. bifidus* Zone.

MATERIAL. **Holotype,** isolated proximal end, PMO NF3369. Other isolated specimens, PMO NF3370–3, are paratypes.

NAME. 'Several-formed.'

DESCRIPTION. This species is based on isolated material, and its important characters relate to features which are probably only to be discerned on such material. However, it is such an important species for understanding the evolution of the astogeny of graptoloids, and its proximal end structure is so singular, as to justify the erection of yet another pendent didymograptid species.

Sicula short, 1·0–1·3 mm long, excluding nema, which we have seen up to 0·4 mm long. Sicular aperture 0·3–0·4 mm wide, with ventral lip up to 0·2 mm long. Theca 1^1 begins high on the sicula, 0·3 mm from its apex (excluding nema), presumably just below the base of the prosicula, and grows alongside the sicula for 0·6–0·75 mm, before swinging outwards and away from the sicula, making an acute angle with it. No more than 0·2 mm of the ventral side of the sicula is free from $th1^1$; the free, curved ventral wall of $th1^1$ extends to 0·8 mm, so that total length of first theca is about 1·4 mm; aperture oval with elongation in the sagittal plane, width 0·4 mm. Foramen for origin of $th1^2$ visible on dissected specimen (Pl. 1, fig. 1) at about halfway along proximal, downgrowing part of $th1^1$, crossing canal passing in front of sicula as a stout tube 0·2 mm in diameter, before curving down in the same fashion as $th1^1$, such that its eventual apertural position is slightly below that of $th1^1$ on the opposing stipe. Origin of $th2^1$ clearly seen on the holotype (Pl. 1, fig. 2) close to proximal end of $th1^2$, such that the ventral walls of the crossing canals form the characteristic arch typical of isograptid development. The width of $th2^1$ is only half that of $th1^2$. On the holotype $th2^1$ curves over on to the back of the first stipe as it would in normal isograptid development. However, at a length of only 0·5 mm this theca terminates with a tiny aperture scarcely more than 0·1 mm in diameter. The next theca on the first stipe originates not from $th2^1$ but from $th1^1$. This is clearly shown on the two best-preserved proximal ends, and is not a pathological development. Hence the proximal two apertures on the first stipe belong to $th1^1$ and $th3^1$, developmentally speaking. Subsequent growth is as usual in pendent didymograptids, although we have no stipes with more than six thecae. Stipe width at first theca only about 0·5 mm, increasing gradually to 1·1 mm at the fifth theca. Apertures are deeply excavated so that more than half of the thecal length lies free, and the angle between the free wall and aperture is a low acute angle distally. Centre tip of each aperture turned out into a short lip. If we take the distance between fifth and sixth thecae to indicate distal thecal spacing this would give 14 in 10 mm. It is probable that the stipes became virtually parallel at the second theca, but the sample is quite inadequate to determine any variation in this character.

DISCUSSION. The proximal end structure described above distinguishes this species from all other graptoloids. The species is unique in that it has two consecutive dicalycal thecae, and yet finishes up with only two stipes, one dichotomy (that producing $th2^1$) having aborted at an early stage. The 'effective' dicalycal theca is $th1^1$, yet the developmental type is initially isograptid; the species can thus be regarded as an intermediate stage in a transition between isograptid and *artus* development. Our two larger specimens (Pl. 1, figs 4, 5) are not as well preserved as the proximal fragments, but neither shows any clear evidence of th2^1, and here development would no doubt be described as of *artus* type. Since all the specimens were recovered from a single small bed, and agree in all other characters, there is no reason to suppose that more than one species is represented. The larger specimens have either passed into *artus* development (i.e. completely suppressed the th2^1 dichotomy), or at a later stage the remnant th2^1 has been resorbed. We regard the species as particularly important in demonstrating the derivation of the *artus* type of development from the isograptid. Moreover it occurs at an appropriate geological horizon, because the pendent species occurring in earlier Arenig strata (where proximal structure is known from good material) have isograptid development, whereas the *artus* development is typical of Llanvirn species.

It would be difficult to recognize the new species without excellently-preserved material. According to Törnquist's original (1879) description of *D. minutus* the sicula of that species is 2 mm long, much longer than in our species. Specimens assigned to *D. minutus* by Bouček (1973) are not so different in sicular length, but the stipes remain consistently narrow; another of Bouček's species, *D. protobifidoides,* reaches a similar distal stipe width, but the thecae are not so deeply excavated, nor are they curved as in our species. Descriptions from flattened material are in general far too schematic to be useful in comparing with our form. Apart from the extra dichotomy, its proximal end structure is generally similar to that of *D. bifidus* (Hall), which underlies it in the Valhallfonna Formation, and it seems reasonable to regard *D. multiplex* as a late derivative of that species, one possibly lying at the root of subsequent pendent didymograptids *(Didymograptus, sensu stricto).*

Didymograptus (Didymograptellus) 'protobifidus' Elles 1933

Fig. 35a–d; Pl. 2, fig. 1

1933 *Didymograptus protobifidus* Elles: 98–99; text-fig. 1 (p. 110); *non* text-figs 2, 3.
1935 *Didymograptus protobifidus* Elles; Benson & Keble: 285–286, text-fig. 3.
1937 *Didymograptus protobifidus* Elles; Ripper: 154–156, text-figs 1, 2, 3, 8.
non 1937 *Didymograptus protobifidus* var. *praecursor* Monsen: 152–153; pl. 3, figs 18, 34; pl. 9, fig. 10; pl. 10, figs 13–15.
1944 *Didymograptus protobifidus* Elles; Decker *(pars)* : pl. 52, fig. 9; pl. 53, fig. 9.
?1947 *Didymograptus protobifidus* Elles; Ruedemann: 343–344; pl. 54, fig. 18.
1960 *Didymograptus protobifidus* Elles; Berry: 63–64; pl. 8, figs 5–9.
1963 *Didymograptus protobifidus* Elles; Ross & Berry: 90; pl. 4, figs 6, 12.
1970 *Didymograptus protobifidus* Elles; Dewey, Rickards & Skevington: text-fig. 3m–p; fig. 4f–h.
?1973 *Didymograptus protobifidoides* Bouček: 80–81.
1976 *Didymograptus protobifidus* Elles; Fortey: 275–276, text-fig. 4a–c.
1977 *Didymograptus protobifidus* Elles; Carter & Churkin: 15; pl. 1, figs 5, 8.
1979 *Didymograptus protobifidus* Elles; Cooper: 71, text-figs 44a–e; pl. 10, figs d–f.
?*non* 1979 *Didymograptus protobifidus* Elles; Mu *et al.*: 58–59; pl. 19, figs 13–20.

Stratigraphic range. ?25, 30–65 m from base in the Olenidsletta Member, below and intergrading with *D. bifidus* (Hall).

Material. Specimens additional to those given in Fortey (1976: 275–276) include PMO NF1846.

Discussion. This species has been described in general terms by Fortey (1976: 275–276) and discrimination from *D. bifidus* has been given in the discussion of that species, and will not be repeated. Since there is perfect intergradation from *'protobifidus'* to *bifidus* passing upwards in the Spitsbergen succession there is no doubt that the earlier form merits taxonomic recognition, and, equally, that it must have had isograptid development and should be included within *Didymograptus (Didymograptellus).* Morphologically homogeneous populations of *D. 'protobifidus'* cover whole bedding planes at about 60 m from the base of the Olenidsletta Member (Pl. 2, fig. 1).

The application of the name *'protobifidus'* needs some justification. The majority of the species given in the synonymy are genuine synonyms of the Spitsbergen form; what is less certain is the identity of this group with the type specimen of *D. protobifidus* Elles from the Skiddaw Slates. Most of the specimens other than the type figured in Elles & Wood (1901) are not of the pendent *Didymograptus* group at all, but are poorly preserved specimens of *Aulograptus,* a feature also noticed independently by J. Riva & C. Jenkins (personal communication). Nor is the exact horizon of the holotype known, although Jackson (1964) records *D.* cf. *protobifidus* from the Arenig part of the Lake District succession. The type specimen, which occurs by itself in the type slab, is too poorly preserved to be sure whether the development is isograptid or not. On the other hand its general dimensions are close to those of the *protobifidus* from Spitsbergen; we see no evidence of tectonic distortion, and the rather coarse lithology in which the type occurs would argue against distortion of the specimen. The name is well established in the literature and it would be difficult to justify using any other name even though some of the critical details are missing from the type specimen. Hence we use the name here, but in quotes to denote our reservations about its true identity.

Extensiform didymograptids

Bouček & Přibyl (1951) proposed the genus *Expansograptus* based on *D. extensus* (Hall) to include extensiform didymograptids. It is clear that the gross rhabdosomal form is not a guide to the true phylogenetic relationships. Even within a species there is variation from horizontal to slightly declined or slightly reclined, and there is as yet too little evidence on proximal end structures to be certain that all generally extensiform didymograptids constitute a monophyletic group. No doubt this is the reason for Bulman (1970) taking the cautious approach of synonymizing *Expansograptus* with *Didymograptus, sensu lato.* We have begun to recognize what we believe are monophyletic groups within graptoloids of didymograptid grade of organization (see *Didymograptellus* above, and *Xiphograptus* below). The use of *Expansograptus* may be justified (although it is still not entirely satisfactory) for those didymograptids with isograptid development, sicula 1–2 mm long forming a relatively broad cone and usually distally curved, and a generally extensiform rhabdosome habit, although this may be with declined or slightly reclined proximal part. We exclude from *Expansograptus* those stout species which are markedly deflexed with the bend at about the 8th to 14th theca, such as *Didymograptus retroflexus* Perner (see Bouček 1973: pls 9, 10), for which the name *Corymbograptus* Obut & Sobolevskaya 1964 may be applicable. This usage of *Corymbograptus* cannot be extended to *all* deflexed species, however, as apparently advocated by Bouček (1973). Examination of populations of such slender deflexed species as *D. nitidus* shows that the amount of deflection at the proximal end varies, and that most characters of the sicula and thecae are like those of *Expansograptus.* This again demonstrates the difficulties of using gross rhabdosomal form as a *sine qua non* in the definition of genera.

Subgenus *EXPANSOGRAPTUS* Bouček & Přibyl, 1951

TYPE SPECIES. *Graptolithus extensus* Hall 1858.

REVISED DIAGNOSIS. Didymograptids with extensiform to slightly declined, deflexed or reflexed rhabdosome habit. Development of isograptid type and dextral mode. Sicula 1–2 mm long, not greatly elongate, lacking virgella, distally curved in the opposite direction to th1^1 so that its aperture is in line with those of stipe series. Theca 1^1 originating high on sicula; th1^1 and th1^2 enclosing an angle ranging from highly acute to almost 180°. Proximal stipe width exceeds 0·5 mm. Rate of expansion of stipes varies widely: may be slow and continuous, or relatively rapid near proximal end with no subsequent increase.

Didymograptus (Expansograptus) extensus (Hall 1858)

Fig. 40a–e; Pl. 6

1858 *Graptolithus extensus* Hall: 132.
1865 *Graptolithus extensus* Hall; Hall: 80–82; pl. 2, figs 11–16.

non 1870 *Didymograpsus extensus* (Hall) Nicholson: 341: pl. 7, figs 2, 2a.
?*non* 1875 *Didymograptus extensus* (Hall); Lapworth *in* Hopkinson & Lapworth: 642; pl. 33, figs 1a–d.
1901 *Didymograptus extensus* (Hall); Törnquist: 14; pl. 1, figs 25–30.
non 1901 *Didymograptus extensus* (Hall); Elles & Wood: 8–9; pl. 1, fig. 1.
1904 *Didymograptus extensus* (Hall); Ruedemann *(pars)*: 668; pl. 14, fig. 1.
1937 *Didymograptus extensus* var. *linearis* Monsen: 115–116; pl. 1, figs 41, 47; pl. 7, figs 17, 20.
1947 *Didymograptus extensus* (Hall); Ruedemann: 331–332.
1960 *Didymograptus extensus* (Hall); Berry *(pars)*: 60–61; pl. 8, fig. 10; *non* pl. 6, fig. 5.
1963 *Didymograptus* aff. *D. novus* Berry; Ross & Berry: 89; pl. 4, fig. 8.
1970 *Didymograptus extensus* (Hall); Dewey, Rickards & Skevington: 32.
?1973 *Expansograptus extensus* (Hall) Bouček *(pars)*: 37–38, text-figs 10a, b; *non* figs 10c–f.
1979 *Didymograptus extensus* (Hall); Cooper: 70; pl. 11b, e; text-fig. 42d.
1979 *Didymograptus extensus linearis* Monsen; Mu *et al.* *(pars)*: pl. 34, figs 1, 2; *non* pl. 33, figs 21, 22.

LECTOTYPE. Here designated **lectotype** is specimen no. GSC 976, original of Hall (1865: pl. 2, fig. 12), and refigured here as Fig. 40d. The associated fauna on the same slab includes *Dichograptus octobrachiatus*, *Sigmagraptus praecursor* and *Phyllograptus ilicifolius*, and some very wide, apparently extensiform graptolite fragments. This assemblage would suggest a horizon in the earlier middle part of the Arenig, above the *T. approximatus* Zone, and possibly also that of *T. fruticosus*.

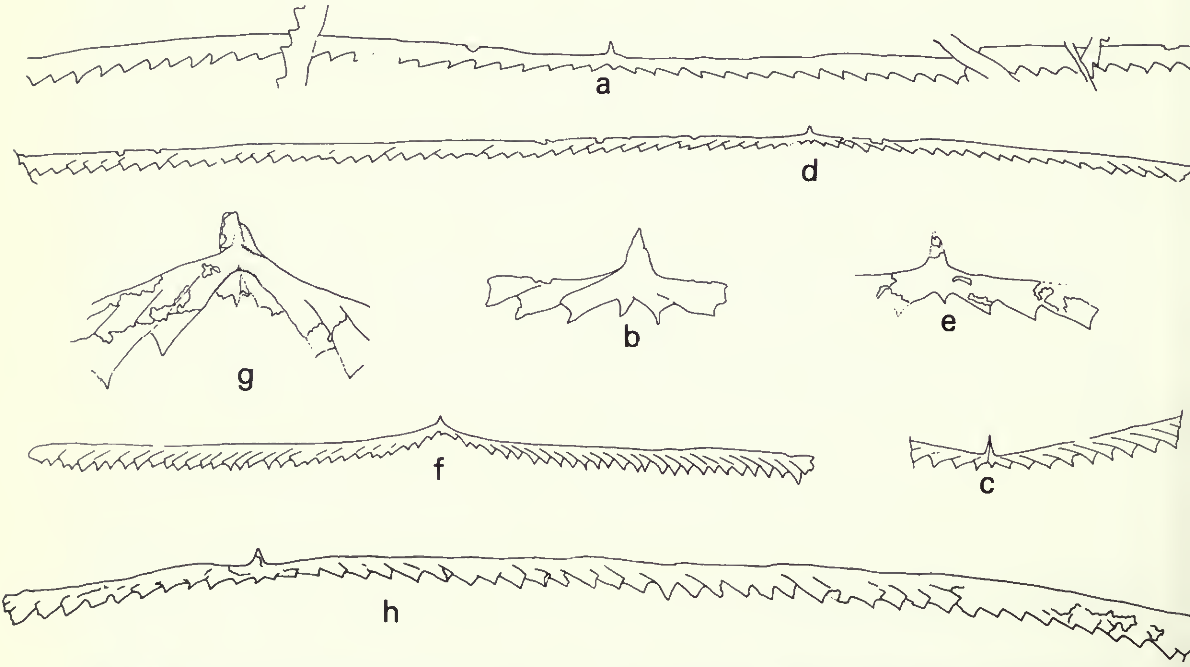


Fig. 40a–e *Didymograptus (Expansograptus) extensus* (Hall). a, SM A105813, part of very large but otherwise typical specimen from slab figured in Plate 5; lower part of Olenidsletta Member in Olenidsletta, 13 m from base; × 3. b, growth stage from same slab as lectotype; × 6. c, PMO NF2535, specimen preserved in relief with distinctly reclined stipes, × 3. d, e, GSC 976, **lectotype** × 3, and enlargement, × 6, of proximal region showing curvature of thecae. Specimen figured by Hall (1865: pl. 2, fig. 12).

Fig. 40f, g *Didymograptus (Expansograptus) nitidus* (Hall). f, GSC 914e, rhabdosome from type series, showing general form; × 3. g, GSC 914d, detail of proximal region preserved in relief, type series, showing isograptid arch and isograptid development type; × 8.

Fig. 40h *Didymograptus (Expansograptus) ensjoensis* Monsen. PMO NF3347, lowest part of Olenidsletta Member, not more than 6 m from base, southern melt stream; × 3.

Stratigraphic range. Lower part of Olenidsletta Member, V_1b, 2 to 75 m from base, corresponding to the upper part of the Bendigonian (three-branched *fruticosus* interval) and the overlying *D. 'protobifidus'* Zone.

Material. SM A109727 (many specimens); PMO NF1764, NF2813.

Description. Both the lectotype and the populations of *D. extensus* from Spitsbergen are very straight extensiforms; there is hardly any hint of declination at the proximal end. We have found only three specimens among Hall's type slabs, and all have this habit, and it is consistent in the larger populations from Spitsbergen; hence we regard this as an important character in taking a strict view of *D. extensus*. The sicula is short, 1·5–1·6 mm long, curved distally, probably with a short lip, so that the aperture lines up with that of th1^2. Theca 1^1 probably had a high origin on the sicula, and distally extends to a point well below the sicular aperture: th1^2 is of similar form, the free walls between th1^1 and th1^2 making an angle of 110°–130°, the point of the sicular profile more or less bisecting this angle. Development isograptid. The stipe expansion diagram (Fig. 41) shows a gradual and continuous increase in width of stipes which is quite characteristic. At the proximal end the stipes are always less than 0·8 mm width measured to the apertural denticles: 0·7 mm is typical. The stipes appear to have continued growing to a great length. Some of the fragmentary stipes on Hall's type slabs are 2 mm broad, and since the longest stipes in contact with the proximal end are only 1·6 mm broad, and this is at th60, it seems probable that individual stipes exceed 20 cm and may have approached 30 cm in length. Proximal thecal inclination is low, 20°–25°, and about 30° distally, with the proportionate amount of thecal overlap increasing in the usual way. Judged from the form they adopt when compressed it is likely that the ventral walls of the distal thecae were embraced by the dorsal walls of the preceding thecae. An important character is that the angle between the free ventral wall of the thecae and its aperture is approximately a right angle; in many other extensiform species this angle is acute. Distance between the apertures of th1^1 and th1^2 is slightly less than 2 mm. Thecal spacing is in general rather low, 8–9 thecae in 10 mm in the distal part of the stipe. Thecae were probably minutely denticulate.

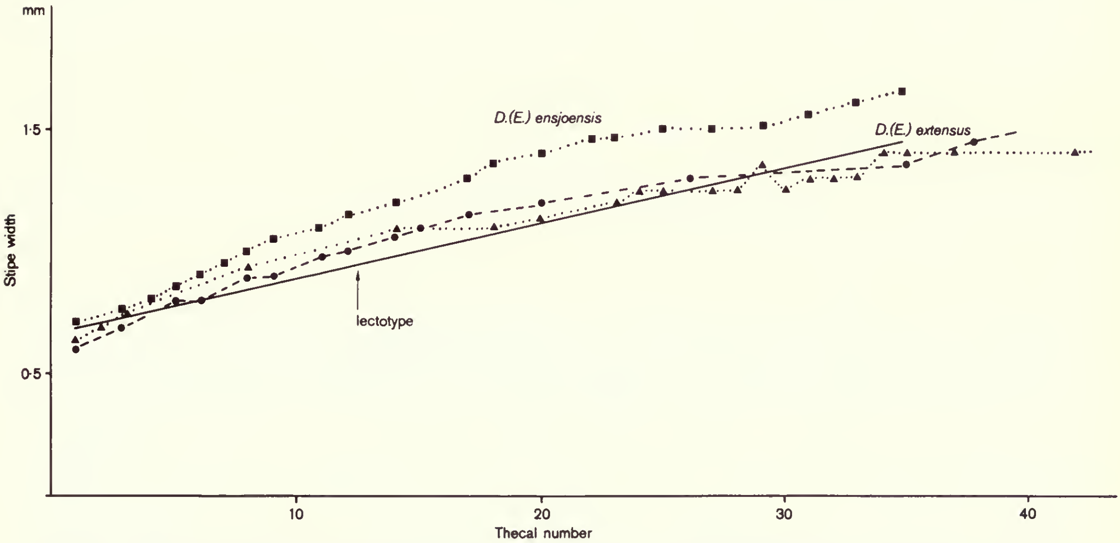


Fig. 41 Stipe expansion diagrams for *Didymograptus (Expansograptus) extensus* and *D. (E.) ensjoensis*. Line is calculated regression from the lectotype of *D. (E.) extensus*.

Discussion. Populations from low in the Olenidsletta Member agree exactly in their proportions and proximal end thecal characters with the lectotype (Fig. 40d). Törnquist (1901: 15) pointed out that the specimens used by Elles & Wood (1901) from the English Lake District to describe *D. extensus* differed both from Hall's types and from Scandinavian specimens in having a distinctly declined proximal portion, after the manner of *D. nitidus*. The immediately straight stipes of *D. extensus* appear to be a consistent character, typifying populations covering large bedding planes in Spitsbergen. The British forms have therefore to be excluded from *D. extensus* (Hall). Bouček's (1973) concept of *D. extensus* seems to be based on the British material, at least as far as his pl. 6, fig. 5 is concerned; however, his text-figs 10a, b appear to have straighter proximal parts, but even here the angle between the free ventral walls of th1^1 and th1^2 appears to be acute, and unlike the type *D. extensus* in this regard. It seems possible that true *D. (Expansograptus) extensus* was absent from the boreal realm during the Arenig.

We have taken a narrow view of *D. extensus* here, that is, we have only identified those specimens which compare closely with the lectotype. As thus constituted the species seems to be confined to the earlier half of the Arenig. Berry (1960) records it as early as the *T. approximatus* Zone, although his figured specimen (1960: pl. 6, fig. 5) shows reclined stipes and apparently acute thecae and is probably not referable here. However, *D. extensus* is certainly characteristic of the *T. fruticosus* and *D. protobifidus* Zones over a wide area of the Pacific Province; Thomas (1960) records it throughout the Bendigonian and Chewtonian of Australia, and Cooper (1979) records a similar range in New Zealand.

Didymograptus (Expansograptus) ensjoensis Monsen 1937

Fig. 40h

Stratigraphic range. Lowest part of Olenidsletta Member, not more than 6 m from base, V_1a, early Arenig (*T. fruticosus* Zone).

Material. PMO NF3347 (several specimens).

Description. *D. ensjoensis* has been rather widely recorded from the earlier part of the Arenig. Monsen's original description gives two photographs and a line drawing; her pl. 7, fig. 12 shows the slightly reflexed profile to either side of the sicula which is displayed on our well-preserved specimen. As Monsen points out, the proximal end structure is much like that of *D. extensus,* and in terms of stipe expansion (Fig. 41) the species is distinguished only by its steeper gradient, representing an earlier attainment of a greater stipe width. The stipe eventually stabilizes in width at about th20–30. Monsen mentions a maximum width of 2·2 mm; in fragmentary distal stipes associated with our specimen with a proximal end, stipes up to 2 mm broad occur. Distal thecal spacing is 9–10 in 10 mm.

As in *D. extensus* the sicula is relatively short, 1·6 mm, in comparison with the eventual stipe width; it is curved away from th1^1. Monsen describes a high origin for th1^1, but our material is too heavily carbonized to be sure of this feature. Theca 1^1 and th1^2 diverge at a high obtuse angle, with the distal part of the sicula hanging down as a small 'tooth' between – a feature well shown also in Monsen's (1937) pl. 7, fig. 14. Width of stipe at the level of the first thecae is 0·70–0·75 mm. Thecal inclination is initially low (about 20°), with correspondingly low thecal overlap. In the distal part of the stipe the preservation suggests that the thecae had by then become very broad tubes, resulting in their imbrication on flattening. As in *D. extensus* the angle between the free ventral wall and the thecal aperture is rarely acute, and usually about a right angle.

Discussion. Harris & Thomas (1940) record *D. ensjoensis* from the Bendigonian of Australia; the proximal end they figure (1940: pl. 2, fig. 15B) compares with our material, although the distal stipe width is said to be 2·5 mm, which is greater than on our material or on the type. Distal thecal spacing is given as 8 in 10 mm, which is a little wider than in the specimens from Spitsbergen. A more closely comparable specimen is figured by Cooper (1979: pl. 11a) from the Bendigonian of New Zealand. Mu *et al.* (1979: 107) record a rather strongly reclined specimen from their zone of *Didymograptus filiformis* in south-west China.

D. similis (Hall 1865) may be confused with this species. The stipe expansion diagram (Fig. 42), incorporating the two of Hall's specimens with proximal ends preserved, shows that *D.*

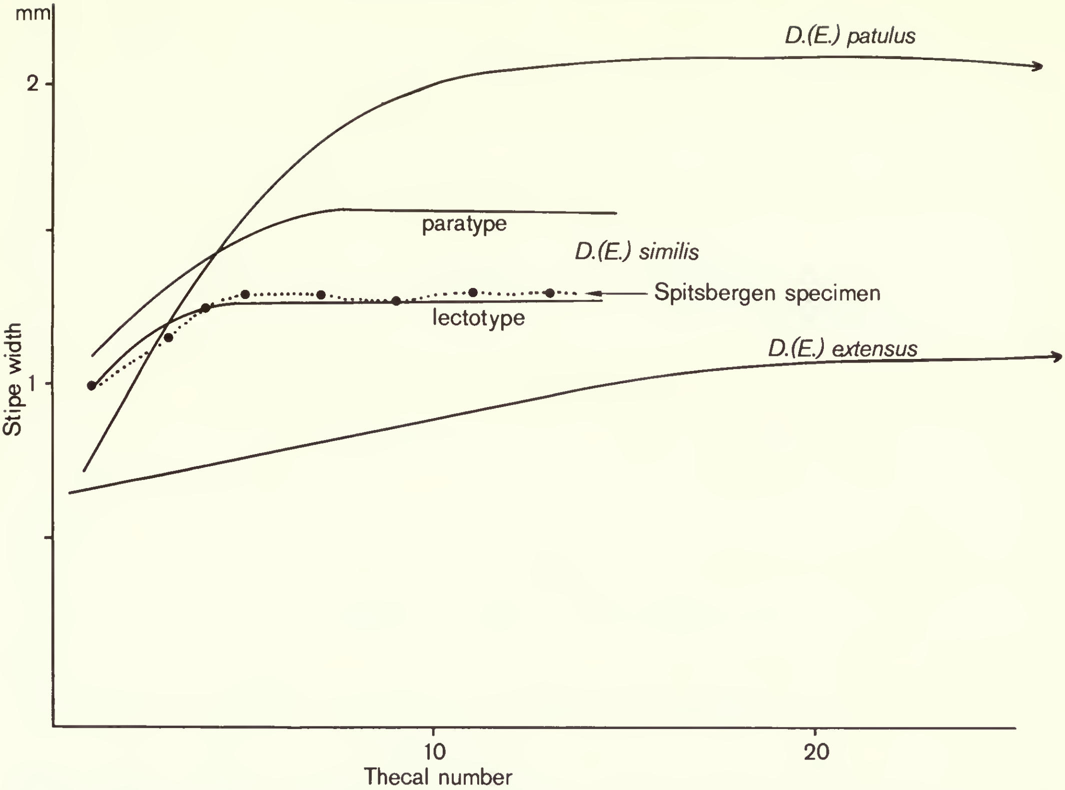


Fig. 42 Stipe expansion diagrams for the extensiform *Didymograptus (Expansograptus)* types of Hall (1865) relevant to the species found in Spitsbergen. Curves fitted by eye. Two type specimens of *similis* give some spread of variation but are of similar growth form; Spitsbergen example shown.

similis has wider stipes proximally, and soon reaches its maximum width, a shape unlike that of *D. ensjoensis*.

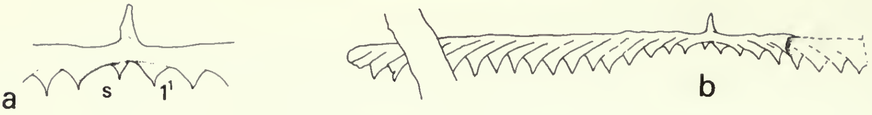
Didymograptus (Expansograptus) praenuntius Törnquist 1901
Fig. 43a, b; Pl. 4, fig. 12

1901 *Didymograptus praenuntius* Törnquist: 17; pl. 2, figs 7–12.
?1937 *Didymograptus praenuntius* Törnquist; Monsen: 118–119; pl. 1, figs 27́, 29.
1938 *Didymograptus asperus* Harris & Thomas: 76–78; pl. 2, figs 25a–c; pl. 4, fig. 23.

STRATIGRAPHIC RANGE. One bed low in the Profilbekken Member, 6 m from base, V_1a, early Arenig (Bendigonian).

MATERIAL. PMO NF475, NF495.

DESCRIPTION. This species has to be discussed in relation to *D. patulus* (Hall), which, as Törnquist (1901) noted, it closely resembles. Only one specimen is suitable to be selected as **lectotype** for *D. patulus*, the original of Hall (1865: pl. 1, fig. 10), GSC 918a, which unfortunately has lost the tip of the sicula. This is shown on Fig. 43c. Hall's type series includes a number of distal stipes, from which some idea of the variability of the species can be obtained. The characteristic features of *D. patulus* include especially the strongly curved thecal form, and the acute 'cut away' appearance of the thecal apertures, so that the free ventral walls of the thecae subtend an acute angle (30°–40°) with the concave apertural margins. The stipe expansion is also highly characteristic, with rapid expansion in thecal length and stipe width



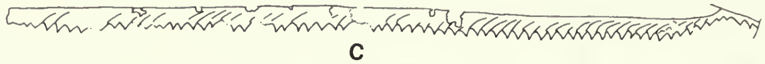


Fig. 43a, b *Didymograptus (Expansograptus) praenuntius* Törnquist. PMO NF475, rhabdosome in full relief, × 3, and enlargement of proximal region, × 6, showing isograptid arch and isograptid development; reverse views. Lowest part of Olenidsletta Member, V$_1$a, type section.

Fig. 43c *Didymograptus (Expansograptus) patulus* (Hall). GSC 918a, **Lectotype**, selected herein; the best preserved of Hall's (1865) original series, the original of his pl. 1, fig. 10; × 1·5.

over the first 6 or so thecae, after which the stipe stabilizes at its maximum width. The specimens here attributed to *D. praenuntius* are similar to *D. patulus* in all these respects, and the stipe expansion has an exactly similar shape (Fig. 44). However, the maximum thickness achieved by the stipes is only about 1·5 mm, and all the stipe fragments in our population are in the range 1·4–1·6 mm. Hall's type series has the range 2·1 to 2·4 mm for stipe width; this variation is accounted for by continued thecal growth, for the apertural profiles are similar in all specimens, and the distance between the dorsal stipe margin and the addorsal margin of the apertures varies betwen 1·5 and 1·7 mm. The same dimension in our specimens lies between 0·9 and 1·1 mm. Törnquist (1901) characterized *D. praenuntius* as having the same form as *D. patulus* but with narrower stipes, and this seems to afford good grounds for our determination. It should be noted that our specimens are in full relief, and it is possible that if flattened the stipes would have become a little wider. Distal thecal spacing on the *D. patulus* type series is 9–11 in 10 mm, and is 9–10 in 10 mm in our population of *D. praenuntius*. The proximal end of one specimen is particularly well preserved (Fig. 43a). The sicula is 1·35 mm long (without preserved nema) and distally curves away from th1^1 in the way we have described as typical of the subgenus *Expansograptus*, so that its aperture is essentially in line with the thecae of the stipe^2. Theca 1^1 commences high on the sicula, and is longer, reflected in the greater length of its free vental wall. Our specimen is in reverse aspect, and well displays the broad (0·3 mm) crossing canal connecting th1^2 and th2^1, showing isograptid development. The angle enclosed between the free ventral wall of th1^1 and th1^2 is about 115°. Thecal apertures are flared, like so many small trumpets, and have a small denticle.

Discussion. Tjernvik (1960) records the range of *D. praenuntius* in the Flagebro drill core from the top of the zone of *Didymograptus balticus* through that of *Phyllograptus densus* to the base of the *Phyllograptus angustifolius elongatus* Zone. This range overlaps that of *Tetragraptus fruticosus,* and it is reasonable to suppose that the Scandinavian occurrences are of the same age as that in Spitsbergen. Monsen's (1937: 118–119) records from Norway may be of the same species, but the stipe widths recorded (1–1·3 mm) are rather narrow. Harris & Thomas (1938) described *D. asperus* from Australia and their description matches that given above for *D. praenuntius* very closely, although their figures are not adequate for satisfactory comparison. Thomas (1960) gives the range of this species as through all except the uppermost Bendigonian, which would accord with the horizon in Spitsbergen. The exact age of Hall's type population of *D. patulus* cannot be determined from associations on the type slabs. Raymond (1914) suggests that it occurs in Zone A at Levis associated with a *T. fruticosus* or *T. approximatus* fauna, which is in general accordance with Berry's (1960) record of *D. patulus* from the *T. fruticosus* and *D. protobifidus* Zones in the Marathon region, Texas. It seems to be an earlier Arenig species, like *D. praenuntius.* Törnquist's (1901) record of *D. patulus* from Sweden at a younger horizon is a misidentification: Chen (*in* Mu *et al.* 1979) has renamed this species *D. patulentis.* If Törnquist's observation (1901: 16) that there was a virgella on his material is correct this species should be referred to *Xiphograptus* gen. nov. (p. 289).

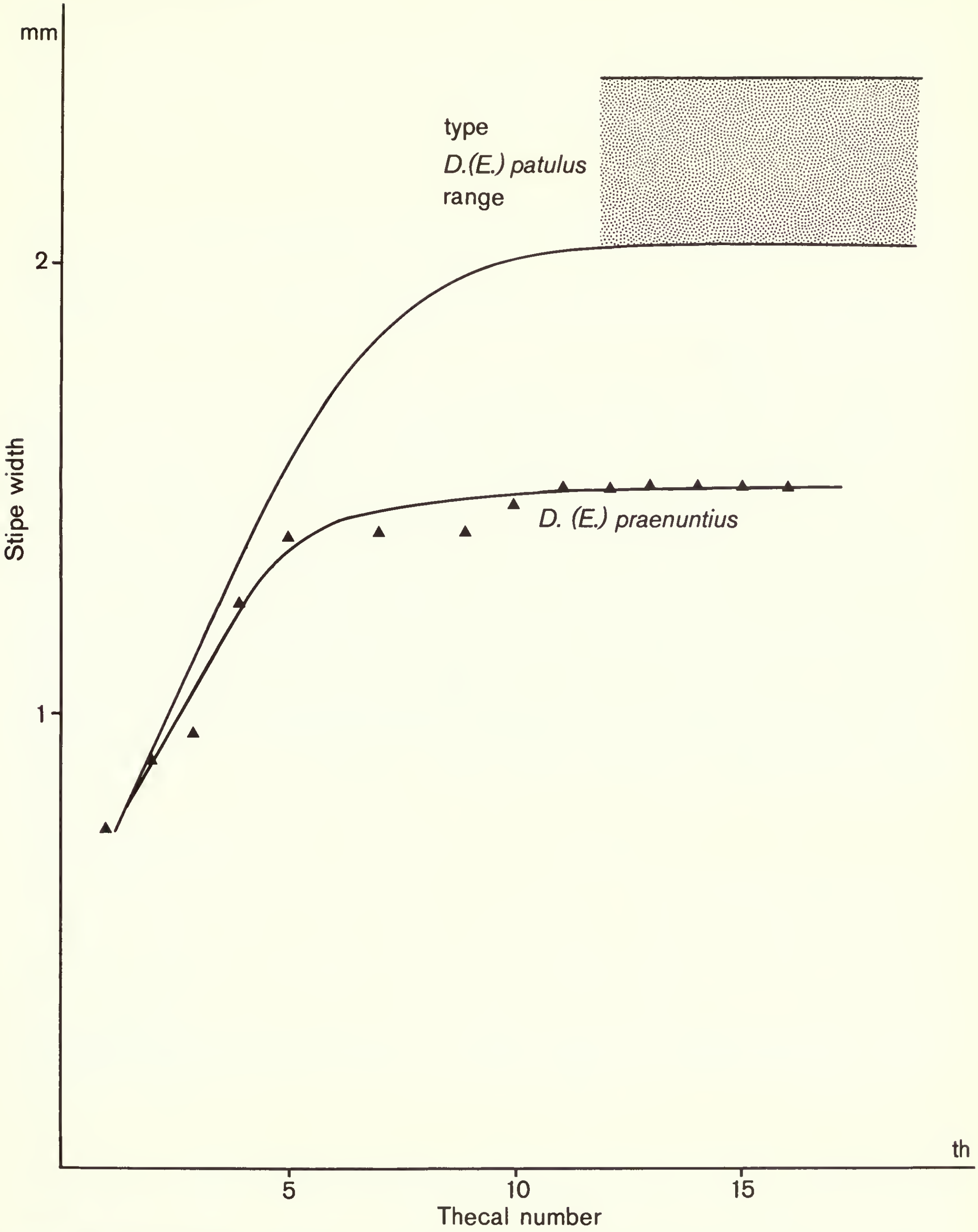


Fig. 44 Stipe expansion diagram for *Didymograptus (Expansograptus) patulus* (Hall) and *D. (E.) praenuntius* Törnquist. Stippled area shows spread of mature stipe widths associated with the type specimen of *D. (E.) patulus* in Hall's collection. Triangles plot best stipe from Spitsbergen.

Didymograptus (Expansograptus) similis (Hall 1865)
Fig. 45a–c

1865 *Graptolithus similis* Hall: 78–79; pl. 2, figs 1–5.
non 1938 *Didymograptus similis* (J. Hall) Harris & Thomas: 76; pl. 2, figs 22a, b; pl. 4, fig. 20.
1979 *Didymograptus constrictus* (J. Hall); Cooper *(pars)*: fig. 42b; pl. 11, fig. f; *non* fig. 42a; pl. 11, fig. d (*constructus* spelling error on plate).

STRATIGRAPHIC RANGE. 17 m from base of Olenidsletta Member, early Arenig, V_1b (latest Bendigonian).

LECTOTYPE. The slab which contains the original of Hall's (1865) pl. 2, figs 2, 3 has on it two specimens of *D. (E.) similis,* one of which is judged to be the original of Hall (GSC 944b) and is here designated **lectotype**. This specimen is not in very good condition, particularly on the ventral side of the proximal end. On the same slab there are specimens of *D. (E.) extensus* and *Tetragraptus serra,* both of which are revised in this paper, and which occur with *D. similis* in Spitsbergen also.

MATERIAL. PMO NF2076.

DESCRIPTION. Rhabdosome horizontal, but with a characteristic gentle convexity to the dorsal stipe margin produced by a slight tendency to reclination on either side of the sicula. Stipes grow to length of about 2 cm. Hall's (1865) pl. 2, fig. 3 shows an apparent arch at the proximal end with no sign of ventral protrusion of the sicula; this was probably a result of the rather poor preservation of the lectotype. The distal part of the sicula protrudes as a small 'tooth' between th1^1 and th1^2, but is very inconspicuous (about 0·25 mm long) rather in the manner of *D. extensus*. Total sicula length is 1·5–1·7 mm, and dorsally it forms a broad cone with the proximal part of th1^1, which must have had a high origin. Growth pattern differs from that of *D. extensus* (Fig. 42): the proximal stipe width at th1^1 is 1–1·2 mm, and there is only a slight increase in stipe width over the first 4 or 5 thecae to a maximum width of 1·25–1·55 mm which remains constant thereafter. Free ventral walls of th1^1 and th1^2 enclose an angle of 110°–130° and are about 1 mm long; the free walls of subsequent thecae are the same length (up to 1·2 mm), with thecae overlapping for about half their length. Thecal inclination is about 25° distally. Angle between ventral wall and apertural margin is usually somewhat acute. At the distal part of the stipe thecal spacing is 9 in 10 mm.

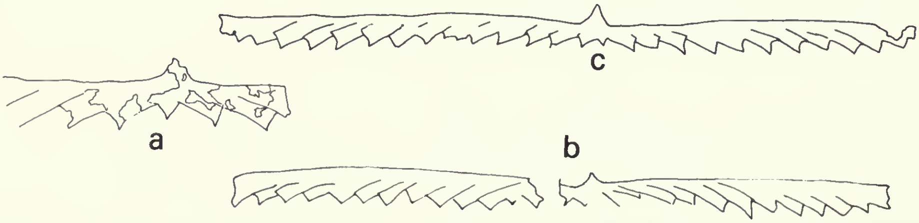


Fig. 45 *Didymograptus (Expansograptus) similis* (Hall). a, b, **lectotype**, GSC 944, proximal region (× 6) and rhabdosome (× 3). c, PMO NF2076, 18 m from base of Olenidsletta Member on Olenidsletta; × 3.

DISCUSSION. Our Spitsbergen specimen compares exactly with the type material. The pattern of growth clearly distinguishes *D. (Expansograptus) similis* from *D. (E.) extensus* which it resembles in proximal end structure. It is very like *D. constrictus* (Hall), which differs significantly only in having the stipe width at th1^1 and 1^2 as wide as 1·7 mm, and attaining a width of 2 mm or more distally. *D. constrictus* appears to be typical of a somewhat earlier horizon (Zone A at Levis) than *D. similis,* and may, of course, intergrade with it stratigraphically. Figures of other North American material of *D. similis* are not good enough to be certain of their identity, although a manuscript note by O. M. B. Bulman records specimens which he states are identical with the types from Bed 2 at Deepkill. Berry (1960) identifies the species from the top of the Bendigonian (three-branched *fruticosus*) through to the Arenig zone of *D. bifidus,* but without figuring specimens. The Australian specimens attributed to *D. similis* by Harris & Thomas (1938) are too narrow proximally and too wide distally to belong to this species. Of the specimens from New Zealand assigned to *D. constrictus* by Cooper one (1979: pl. 11, fig. f) has the proportions of *D. similis*; this is from the *D. protobifidus* Zone. A contemporaneous group of Scandinavian species centred on *D. suecicus* Tullberg 1880 may well prove to be close to *D. similis*, but the revision of these species is beyond the scope of this paper.

Subgenus ***CORYMBOGRAPTUS*** Obut & Sobolevskaya, 1964

TYPE SPECIES. *Didymograptus v-fractus* Salter 1863.

DISCUSSION. This subgenus is used with many reservations. As originally proposed by Obut & Sobolevskaya (1964) it was simply an upgrading of the old informal division by Elles & Wood of 'deflexed didymograpti'. There is no proof that the deflexed species constitute a monophyletic group, nor is our material from Spitsbergen sufficiently well preserved to decide whether there are any characters of the proximal end of the type species which might define a natural group. There is evidence to suggest that the deflexed species were produced by several 'bursts' at different times. In the European Arenig the abundant deflexed forms (*Didymograptus v-fractus, D. uniformis, D. vacillans, D. v-similis* and *D. deflexus*) are generally present low in the series, as they are in our successions in Spitsbergen and in Scandinavia. In south-west China (Mu *et al.* 1979) a whole range of deflexed species (purportedly 24 species) occurs along with the Arenig pendent *Didymograptus (Didymograptellus)* radiation and true *Phyllograptus* (as restricted in this paper), which indicates a mid-Arenig age, and there is no reason to suppose that this group of species is related to the earlier ones from Europe. In the later part of the Arenig (*D. hirundo* Zone and Castlemainian–Yapeenian) deflexed species are generally scarce, but one species which is very widespread in the Pacific Province is *Didymograptus v-deflexus* Harris (1924; see also *Corymbograptus v-fragosus* Obut & Sobolevskaya 1964), a gracile species with a short sicula which may be unrelated to any of the earlier forms. Finally, in the Llanvirn of Bohemia Bouček (1973) has described a series of robust species (*C. retroflexus* Perner 1895 and various subspecies, together with *C. imminutus*); if Bouček's (1973: 54) attribution of *artus* development to these is correct then it is probable that this group is more closely related to the Llanvirn pendent species *Didymograptus (Didymograptus)* than to earlier deflexed species.

Furthermore there are several species, *D. nitidus* Hall being one, in which the degree of deflection varies within wide limits. The variation extends from forms with marked change in direction of stipe growth, through those weakly declined, to those in which a gentle bend occurs at the sixth or seventh theca. Bouček (1973) assigns *D. nitidus* to *Expansograptus,* as he does *Didymograptus simulans* Elles & Wood 1901, even though both would fit his definition of *Corymbograptus*: 'stipes at first pendent, later, at some distance from the sicula, flexing sideward at an obtuse to straight angle' (1973: 49). It is obvious that a 'genus' which may have had as many as four separate origins, and into which the placing of certain species is almost impossible to decide, is scarcely a useful taxonomic category at the moment. Our use of it here is based on the type species, and the early Arenig deflexed group.

Didymograptus (Corymbograptus) v-fractus Salter 1863

Fig. 46c; Pl. 2, fig. 5

STRATIGRAPHIC RANGE. Lower part of Olenidsletta Member, 13–20 m above base, V_1b, early Arenig (late Bendigonian).

MATERIAL. PMO NF3364.

DISCUSSION. The one specimen is not well preserved, but it is of importance in providing a link with the earlier Arenig succession of the English Lake District. Distal thecal spacing is 10 in

10 mm, at the upper limit of the range given by Elles & Wood (1901: 34). Our stipes do not greatly exceed 3 cm in length; the specimens used by Elles & Wood to illustrate the species have a stipe width of 2 mm or slightly more at this length, which is the same as on our specimen. Examples with generally similar form have been figured by Monsen (1937: pl. 10, figs 6, 7), from the zone of *Phyllograptus densus* in Norway. The maximum abundance of deflexed didymograptids in the Lake District is in the earlier half of the Arenig series, and according to Jackson (1962) the stouter species, compared by him with *D. v-fractus,* are confined to the earliest zone, that of *D. deflexus.*

Didymograptus (Corymbograptus) cf. ***deflexus*** Elles & Wood 1901
Fig. 46a, b

Stratigraphic range. Olenidsletta Member, 6–21 m from base, V_1b, early Arenig (late Bendigonian).

Material. PMO NF2395a, NF2804.

Discussion. Several deflexed specimens from the earlier part of the Olenidsletta Member are included here. They are more slender than *D. v-fractus,* and with 13 thecae in 10 mm distally. Elles & Wood's (1901: 36) description of *D. deflexus* implies that the distal stipe width of their species was only 1 mm (ours are 1·3–1·4 mm); hence our identification is qualified. However, it is possible to find specimens from the Lake District (for example BM(NH) no. P.7159) with identical distal stipe width and thecal spacing to those of our specimens, and it seems probable that there is more variation in *D. deflexus* than Elles & Wood allowed. *Didymograptus* cf. *deflexus* of Monsen (1937: 146) is also very close to our material.

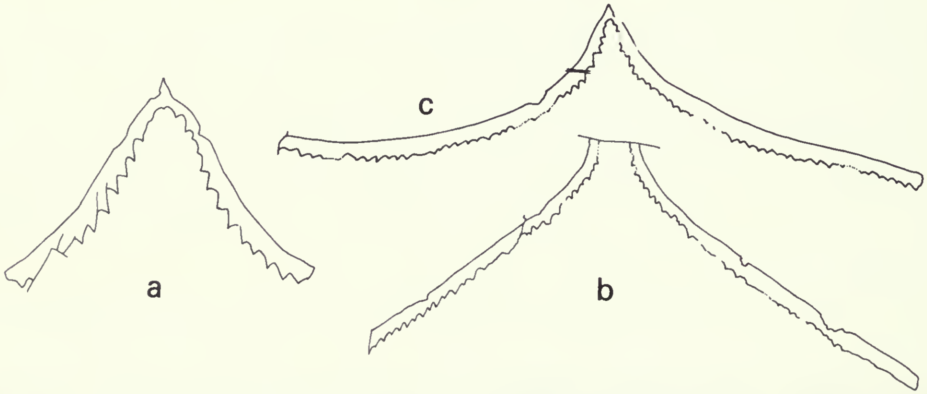


Fig. 46a, b *Didymograptus (Corymbograptus)* cf. *deflexus* Elles & Wood. a, PMO NF2395a, proximal part of rhabdosome; × 6. b, PMO NF2804, poorly preserved incomplete specimen, showing characteristic distal declination of stipes; × 2. 6 m from base of Olenidsletta Member on Olenidsletta.

Fig. 46c *D. (C.) v-fractus* Salter, PMO NF3364, 13–20 m above base of Olenidsletta Member, Olenidsletta; × 2.

Didymograptus (sensu lato), cf. ***D. pennatulus*** Hall 1865
Pl. 4, fig. 9

Stratigraphic range. Upper part of Olenidsletta Member 140 m above base, V_3, late Arenig, *Isograptus victoriae victoriae* Zone.

Material. PMO NF3377–8.

Discussion. This very broad species occurs in one bed high in the Olenidsletta Member. It is preserved in full relief. We know it was an extensiform didymograptid, because a very poor proximal end which could not be collected was observed in the field. Maximum stipe width was evidently attained rapidly and maintained over long distances (greater than 8 cm). The widest specimen is over 6 mm broad; thecae are long and curved, the apertural margin being almost parallel to the dorsal stipe wall. There are long apertural denticles. In a narrower specimen, 4·5 mm broad, the distal curvature of the thecae is not completed, and the apertures are still oblique, indicating that there was variation within the population in the ultimate width of the stipes. Specimens resembling the narrower one have been referred to as *D. hirundo.* The best comparison is with Hall's (1865) species *D. pennatulus,* which has similar stipe widths, according to Ruedemann (1947). However, forms which have been attributed to *D. pennatulus* apparently have a very long stratigraphical range, from the earlier part of the Arenig probably into the Llanvirn, and we doubt that all records represent the one species. Since the pendent didymograptids evidently produced massive 'overgrown' species on several occasions, we see no reason why this should not apply to extensiform species as well. Our determination is accordingly tentative.

Genus *PSEUDOPHYLLOGRAPTUS* nov.

TYPE SPECIES. *Phyllograptus angustifolius angustifolius* Hall 1858.

DIAGNOSIS. Quadriserial, scandent rhabdosome with four stipes united along their dorsal margins; median septa separating adjacent thecal series cruciform, imperforate; proximal development isograptid, dextral; initial thecae distally declined or horizontal, sicula lacks virgella.

NAME. Referring to the superficial similarity between the new genus and *Phyllograptus, sensu stricto.*

DISCUSSION. Dichograptids with phyllograptoid rhabdosomes in which the median septa are complete (imperforate) and more or less cruciform in cross section are here transferred to the new genus *Pseudophyllograptus,* with *Phyllograptus angustifolius angustifolius* as type species. The type material of *P. a. angustifolius* is redescribed here but the diagnostic characters of the genus are revealed only by relief material such as that from Sweden (*P. a. angustifolius*; Holm 1895) and Spitsbergen (*P. angustifolius chors* subsp. nov., p. 244). Isograptid development was inferred from a series of serial sections of the Swedish form by Bulman (1936*a*), and is also inferred from serial sections for the material from Spitsbergen described here, where overall development of the rhabdosome follows the *T. bigsbyi* plan.

Where the internal rhabdosome structure is unknown, the following may prove useful in distinguishing the genus from *Phyllograptus.* The distal portions of the first pair of thecae, 1^1 and 1^2, are pendent or horizontal rather than growing upwards as in *Phyllograptus,* and they lie in the interangle between the two stipes on each side rather than forming part of the second-order stipes themselves, as in *Phyllograptus typus*: see p. 280. The rhabdosome has a more rounded proximal end and a more nearly parallel-sided outline; thecae throughout the rhabdosome have a higher initial angle of inclination to the long axis of the rhabdosome and

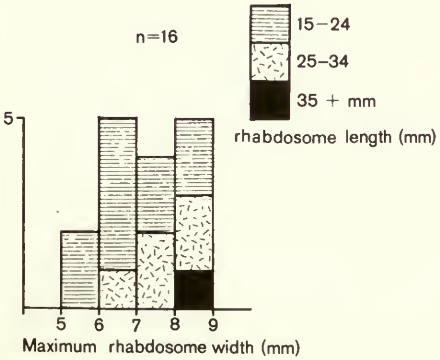


Fig. 47 *Pseudophyllograptus angustifolius angustifolius* (Hall), type population; frequency distribution of rhabdosome width (taken to nearest whole number). Rhabdosome length shown by pattern; note that longer rhabdosomes have greatest width.

are less curved, especially in the proximal part of the rhabdosome. Even if only fragmentary three-dimensional material is available a transverse section of the axial region should reveal the cruciform median septum.

SPECIES AND SUBSPECIES. *Phyllograptus angustifolius* Hall 1858, *P. a. elongatus* Bulman 1931, *Pseudophyllograptus angustifolius chors* subsp. nov., *Pseudophyllograptus angustifolius* subsp. 1, *Phyllograptus densus* Törnquist 1879, and *P. typus* var. *parallelus* Bulman 1931.

In addition to *Pseudophyllograptus angustifolius chors* and the nominate subspecies, diagnostic rhabdosome structure is also present in a specimen here attributed to *Phyllograptus densus* Törnquist from Kinnekulle, held by the New Zealand Geological Survey, and preserved in partial relief. *P. typus* var. *parallelus* Bulman 1931 and *P. angustifolius elongatus* Bulman 1931 are included on grounds of their relatively straight and highly inclined thecae, particularly in the proximal part, combined with an approximately parallel-sided rhabdosome. Judged from their published photographs, several of the phyllograptoids described by Mu *et al.* (1979) are likely to belong to *Pseudophyllograptus*.

Pseudophyllograptus angustifolius angustifolius (Hall 1858)

Fig. 48e, f

1858 *Phyllograptus angustifolius* J. Hall: 139.
1865 *Phyllograptus angustifolius* Hall; J. Hall: 125; pl. 16, figs 17–21.

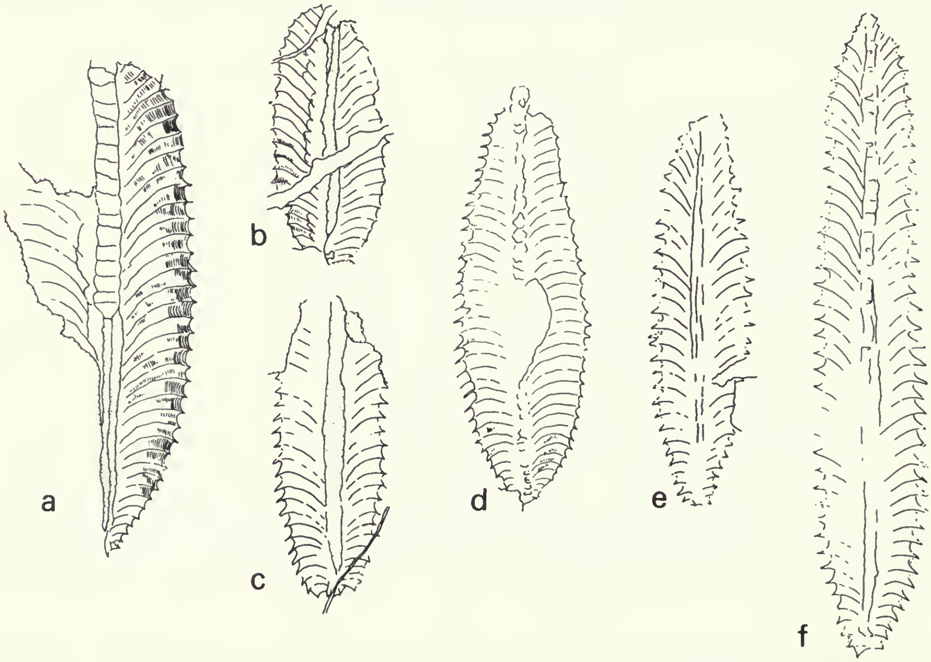


Fig. 48a–c *Pseudophyllograptus angustifolius chors* subsp. nov. a, PMO NF1493, **holotype,** specimen preserved in relief in limestone; upper thecal series broken away exposing, in the lower part of the rhabdosome, the median septa (stippled) which are imperforate, distinguishing the form from *Phyllograptus, s.s.* Growth striations diagramatic. Olenidsletta Member, 103 m above base. b, NF1548, specimen in full relief in limestone. Olenidsletta Member 100·8 m above base. c, NF1513, showing highly inclined, curved proximal thecae. Olenidsletta Member, 101·9 m above base. All × 2.

Fig. 48d *P. angustifolius* subsp. 1, PMO NF3361, specimen preserved in relief, from 8·5–10 m above base of Olenidsletta Member, i.e. the earliest phyllograptoid in the Spitsbergen sequence; × 2.

Fig. 48e, f *Pseudophyllograptus angustifolius angustifolius* Hall. e, GSC 939a, paratype, flattened, in black shale, figured by Hall (1865: pl. 16, fig. 19). f, GSC 939b, **lectotype,** flattened, in black dolomitic shale, figured by Hall (1865: pl. 16, fig. 21). Both × 2.

1895*a* *Phyllograptus angustifolius* Hall; Holm: 488–489; pl. 14, figs 1–12.
1902 *Phyllograptus angustifolius* Hall; Elles & Wood: 100–101: pl. 13, figs 7a–f.
?1904 *Phyllograptus angustifolius* Hall; Ruedemann: 711–714, text-fig. 37; pl. 15, figs 31–34.
1936*a* *Phyllograptus angustifolius* Hall; Bulman: 39–44, text-figs 13–15; pl. 1, fig. 26; pl. 4, figs 7–10.
?1947 *Phyllograptus angustifolius* Hall; Ruedemann: 315–316; pl. 53, figs 2–6.
?1947 *Phyllograptus angustifolius* var. *magnificus* Ruedemann: 316; pl. 53, fig. 7; pl. 90, fig. 20.

LECTOTYPE. GSC 939b, figured by Hall (1865: pl. 16, fig. 21) and refigured here (Fig. 48f) is here designated **lectotype**. It is held by Geological Survey of Canada, Ottawa.

PARALECTOTYPES. GSC 939, 939a, containing the specimens figured by Hall (1865: pl. 16, figs 17–21), one of which is refigured here (Fig. 48e), together with more than 25 other rhabdosomes. All rhabdosomes are preserved as flattened carbonaceous films; all material held by Geological Survey of Canada, Ottawa.

HORIZON. Several biserial forms are present in slab GSC 939b, including *Pseudoclimacograptus* of *eximius* Ruedemann type, ?*Cryptograptus inutilus* (Hall), together with *Pseudisograptus* (*dumosus* or *nanus*), suggesting Zone D of the Levis succession.

DESCRIPTION OF TYPE MATERIAL. Details of proximal structure and development and of internal rhabdosome structure are unknown. Rhabdosomes are approximately parallel-sided and elongate when mature and are generally tapered to a rounded termination at both proximal and distal ends. The longest rhabdosome, the lectotype, is 42 mm long. Rhabdosomes are generally widest at about 10 to 15 mm from the proximal end and thereafter remain parallel-sided or taper very slightly. Maximum rhabdosome width ranges widely, from 5·5 mm to 8·5 mm; the wider forms tend also to be the longer forms (Fig. 47). Up until the widest point of the rhabdosome, thecae are moderately curved and highly inclined, and they become progressively less inclined, particularly in their initial growth, as the distal rhabdosome margin is approached. Apertural margins are deeply recessed in outline giving a denticulate appearance to the projecting ventral thecal margin. Thecae are spaced 8½ to 12 in 10 mm in the middle third of the rhabdosome, strongly modal at 10–11 (Fig. 49).

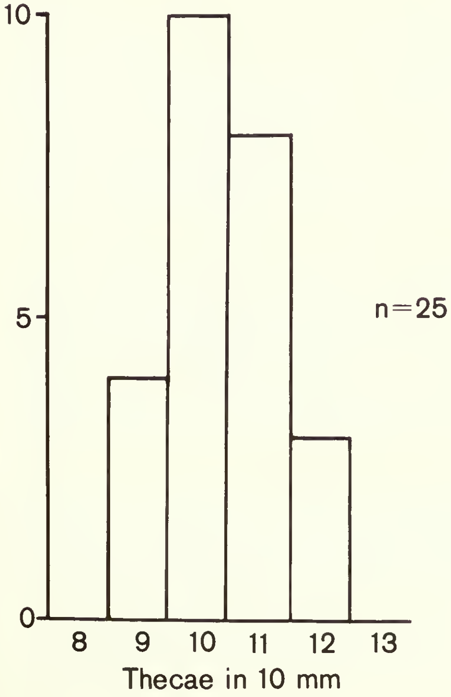


Fig. 49 *Pseudophyllograptus angustifolius angustifolius* Hall, type population; frequency distribution of mature thecal spacing (taken to nearest whole number).

Discussion. The range in thecal spacing is greater than that usually allowed for the species and the mode somewhat lower (e.g. Ruedemann 1947 and Elles & Wood 1902 both give 11–13 thecae in 10 mm). Mature rhabdosomes are readily distinguished by their approximately parallel sides and high inclination of proximal thecae; immature rhabdosomes are distinguished from similar-sized rhabdosomes of *Phyllograptus ilicifolius* by the high initial angle of inclination, and lack of strong curvature, of proximal thecae.

Details of internal rhabdosome structure and proximal development, indeterminable from the type material, can be inferred by reference to the well-known and beautifully preserved material from Sweden, described by Holm (1895), Bulman (1936*a*) and Skevington (1965). The Swedish material, from Skevington's work, comes from the uppermost *hirundo* Zone of the Orthoceratite Limestone and is accompanied by the earliest diplograptids of the Swedish succession, including *Cryptograptus austrodentatus oelandicus* Bulman, indicating a similar stratigraphic horizon to that of the type material at Levis. Initial thecal budding conforms with the isograptid type of development (Bulman 1936*b*) and the septa separating the four thecal series in the axial region are complete (Holm 1895) and not perforated as in *Phyllograptus, s.s.* Details of thecal morphology and growth line data are clearly shown by Skevington (1965: figs 14–16).

Although *P. angustifolius* is most widely recorded from strata of latest Arenig or Llanvirn age around the world it is also commonly recorded from the mid or early Arenig (e.g. Texas, Berry 1960; Australia, Thomas 1960; New Zealand, Cooper 1979; England, Jackson 1962; China, Mu *et al.* 1979). The evidence from Spitsbergen, however, suggests that the earlier Arenig forms represent a distinct subspecies and until their detailed morphology is known they should be regarded only as *P. angustifolius, sensu lato.*

Because Ruedemann's (1904) figured material is said to come from Beds 2–6 of the Deepkill section it is possible that the earlier subspecies is also embraced by it. Ruedemann's var. *magnificus* from the Blakeley sandstone in Arkansas (of *G. dentatus*, or *P. tentaculatus*, Zone age) appears to differ in no significant way from the nominate subspecies, but the scales given for the two illustrations (1947: pl. 53, fig. 7 and pl. 90, fig. 20) of the cotype are inconsistent and there is thus some doubt about true dimensions and thecal spacing.

Pseudophyllograptus angustifolius chors subsp. nov.

Fig. 48a–c; Pl. 4, fig. 6

Stratigraphic range. 100·8 to 103·3 m above base of Olenidsletta Member, uppermost V_2 and V_3a, Castlemainian.

Material. **Holotype,** PMO NF1493 (two counterparts, in relief); paratypes PMO NF1446, NF1506–7, NF1513, NF1548, NF1617, NF3295 and seveal other specimens. Also serially ground specimens PMO NF3174–5.

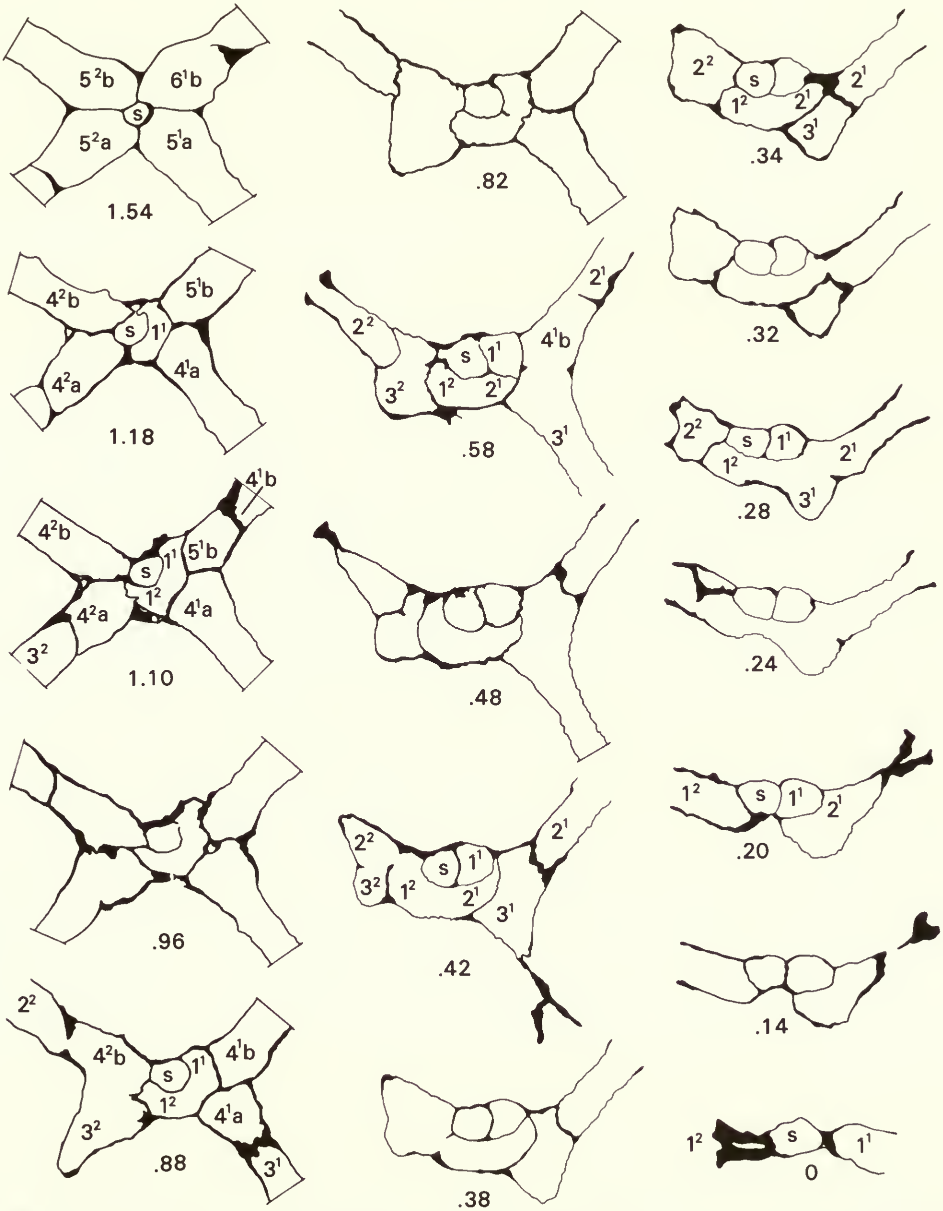
Name. 'A walled enclosure,' referring to the enclosure of the sicula within the rhabdosome.

Description. Rhabdosome elongated, oval to elliptical, up to 35 mm long, and 13 mm in maximum width; the width to length ratio is 0·35 to 0·45. In the axial region of the rhabdosome thecae are 1·8 mm in lateral width and moderately transverse in cross section. They are inclined initially at 45° to 55° and curve out to about 90° near their apertures. Their apertural margins are extended into a lip, giving a denticulate appearance in the flattened rhabdosome. Initial thecae are highly inclined. Thecal spacing, measured in 4 specimens only, is 8·5–11 (8·5, 10·5, 11, 11) in 10 mm.

Internally the median septum is unperforated and in cross section is like that described by Holm (1895: pl. 14, figs 11, 12) in the Swedish form; the opposing stipes ^{2}a and ^{1}b are united over a short lateral distance along their dorsal margins separating the two sides of the cross by a short bar (Fig. 51). The median septum is clearly exposed in the lower half of the holotype, PMO NF1493 (Fig. 48a).

Description of section series. The proximal end of specimen NF3175 was serially ground at intervals ranging from 0·02 to 0·05 mm, and the ground surfaces were drawn under camera lucida and photographed. An excellent series of sections resulted revealing the proximal structure and development of the rhabdosome. A selection of these is shown in Fig. 50.

Overall sicula length is a little greater than that represented in the ground section series, i.e. about 1·8 mm; dorsoventral width of the sicula is 0·2 mm; lateral width 0·15 mm near the


5^2b
6^1b
s
5^2a
5^1a
1.54
4^2b
5^1b
s
1^1
4^2a
4^1a
1.18
4^1b
4^2b
1^1
5^1b
s
1^2
4^2a
4^1a
3^2
1.10
.96
2^2
4^2b
1^1
4^1b
s
1^2
4^1a
3^2
.88
3^1
.82
2^1
2^2
4^1b
s
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1^2
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3^1
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.48
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.32
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1^2
3^1
.28
.24
1^2
s
1^1
2^1
.20
.14
1^2
s
1^1
0

Fig. 50 *Pseudophyllograptus angustifolius chors* subsp. nov. Selected serially ground sections through the proximal region of specimen PMO NF3175, from 100·8 m above base of Olenidsletta Member, type section; × 17. Section level indicated by number (in millimetres) above basal section. The highest section, at 1·54 mm above base, shows the sicula entirely enclosed by thecae 5^2a, 5^2b, 6^1b and 5^1a (hence *chors,* enclosure). The foramen between th1^2 and th2^1 extends from about section 1·18 to section 0·58, that is for 0·4 mm. Note that the distal portions of thecae 1^1 and 1^2 lie medially between the sagittal planes of the four thecal series (stipes) as seen in higher sections (e.g. section 1·54).

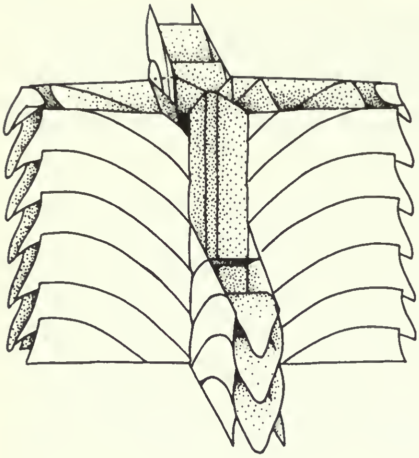


Fig. 51 *Pseudophyllograptus angustifolius chors* subsp. nov. Cut-away diagram showing internal rhabdosome structure.

aperture. The ventral side of the sicula was not determined and it is not known on which side of the sicula the first theca develops. Theca 1^1 arises 0·36 mm below the apex of the sicula and, at 0·56 mm from the apex, expands to envelop about half of the sicula (in transverse section; Fig. 50, section 1·18). Theca 1^2 arises high on th1^1 and the $1^1/1^2$ interthecal wall appears at about 1·0 mm from the apex of the sicula. Thecae 1^1 and 1^2 then grow in contact with the sicula to the level of the sicular aperture, where they turn abruptly outwards to become horizontal. The insertion of subsequent thecae, as inferred from the section series, is shown in the thecal diagram (Fig. 52). Initial development is dextral and isograptid, with th1^2 dicalycal. On the stipe^1 side the dicalycal theca, th3^1, is right-handed and dichotomy is isograptid. On the stipe^2 side, the dicalycal theca 3^2 is left-handed and dichotomy is also isograptid. Development of the rhabdosome thus follows the same plan as that of *Tetragraptus bigsbyi* (Bulman 1970).

Thecal budding sequence differs from that described by Bulman (1936*a*) in *P. angustifolius angustifolius* from the Orthoceras Limestone of Sweden, where the two second-order dichotomies were thought to conform with what is here termed the *artus* type of division rather than isograptid as described here. However, Bulman's interpretation was based on a comparison with *T. bigsbyi* which has since (Bulman 1955, 1970) been reinterpreted. If *Phyllograptus angustifolius* is similarly reinterpreted then its thecal budding sequence conforms with that described here.

In the initial downward growth of thecae 1^2, 2^1 and 2^2, the Spitsbergen form differs from that of Sweden (Bulman 1936*a*: text-fig. 15), where these thecae are shown as having no initial downward component of growth. A further difference lies in the way the sicula becomes entirely enclosed within the rhabdosome during its scandent development (hence *chors,* enclosure) rather than remaining, as a protruding structure, along the lateral wall at the junction of stipes ^{1}b and ^{2}b (compare Bulman's sections in his text-fig. 13B with those given here in Fig. 50).

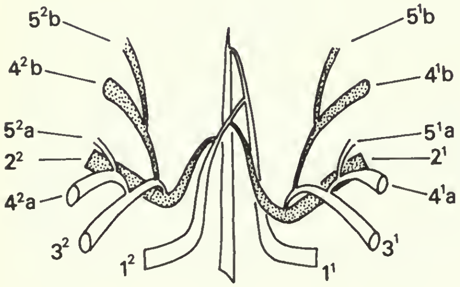


Fig. 52 *Pseudophyllograptus angustifolius chors* subsp. nov. Thecal diagram; stipes ^{1}b and ^{2}b stippled.

DISCUSSION. There appears to be a much more limited range of variability of rhabdosome shape and proportions than in *Phyllograptus typus*. The new subspecies is based on differences in proximal structure compared with the Swedish *P. angustifolius angustifolius* as described above. In his discussion of the Swedish subspecies Bulman (1936*a*) found several points of difference in proximal development and structure from *Tetragraptus bigsbyi* and concluded that the latter was unlikely to be the ancestor of the former. The Spitsbergen form conforms much more closely to *T. bigsbyi,* as interpreted by Bulman (1970), and a reclined tetragraptid of *bigsbyi* type is a feasible ancestor for it.

The Swedish and Spitsbergen forms, along with the form described here as subsp. 1, are all referred to Hall's species *angustifolius,* implying that the total range of the species *s.l.* is from lower Arenig to topmost Arenig or basal Llanvirn. However, it is quite possible that, as the pseudophyllograptid rhabdosome represents merely a reclined tetragraptid with its stipes united along their dorsal margins, it has been repeatedly derived from tetragraptid ancestors at different times. Such a derivation would, if it could be proved, carry important implications for taxonomy and nomenclature of the group.

Pseudophyllograptus angustifolius subsp. **1,** nov.

Fig. 48d; Pl. 4, fig. 8

STRATIGRAPHIC RANGE. The only specimen comes from the 8·5–10 m interval in type section, Olenidsletta Member V_1b.

MATERIAL. PMO NF3361a and b (counterparts), well preserved in semirelief.

DISCUSSION. The form differs from *Pseudophyllograptus angustifolius chors* subsp. nov. only in the less curved and more highly inclined thecae, particularly noticeable in the distal part of the rhabdosome. However, because the specimen comes from an earlier horizon than is generally recorded for *P. angustifolius, s.l.,* and the Spitsbergen section is separated from other pseudophyllograptids by a considerable gap (Fig. 1, p. 161), it seems unwise to include them in *P. angustifolius chors* and so greatly extend the range of that subspecies. It is probably a distinct subspecies but is best left in open nomenclature because little is known of its proximal structure.

Genus ***PSEUDOTRIGONOGRAPTUS*** Mu & Lee, 1958

TYPE SPECIES. *Graptolithus ensiformis* Hall 1865.

DISCUSSION. The taxonomic history of the graptolites that were formerly included in *Trigonograptus ensiformis* (Hall) is complicated. Jackson & Bulman (1970) showed that the holotype of the type species of *Trigonograptus, T. lanceolatus* Nicholson, was a specimen of *Didymograptus* preserved in an unusual way. *Tristichograptus* was proposed as a new name, with the well-known species *T. ensiformis* (Hall) as type species. Fortey (1971) described some beautifully preserved isolated material attributed to *T. ensiformis* from the Valhallfonna Formation, which had a unique triserial scandent arrangement of the stipes. He indicated that the genus *Pseudotrigonograptus* Mu & Lee 1958 (type species, *M. uniformis* Mu & Lee 1958) might prove to be a senior synonym of *Tristichograptus.* Rickards (1973) accepted this, and essentially synonymized most of the described species of *Trigonograptus* with *T. ensiformis* (Hall), including the designated type species of *Pseudotrigonograptus.* So in Rickards' opinion the type species of *Pseudotrigonograptus* is *P. ensiformis* (Hall). Our additional material from Spitsbergen represents triserial and quadriserial forms of *'ensiformis'* type, both of which have previously been reported from China (Mu & Zhan 1966). The quadriserial form makes its first appearance, as one might expect, just below the earliest triserial form. We believe that the quadriserial *'ensiformis'* deserves specific distinction from the triserial one. The problem is that the usual mode of preservation of the flattened material, which is essentially along the septum between thecae, showing no apertures (Fortey 1971: fig. 2), does not reveal direct evidence of the whole form of the rhabdosome. In our opinion the unifying character of these graptolites is the side-by-side arrangement of the scandent stipes, which is unlike the cruciform disposition of *Phyllograptus* and *Pseudophyllograptus,* and indicates a monophyletic origin of both three- and four-stiped scandent forms. Regardless of the number of species the valid generic name is *Pseudotrigonograptus.* The four-stiped form is both wider (across two rows of thecae) and longer than the three-stiped form; the type material of *T. ensiformis* (Hall) is of this kind, and probably had four series of thecae (Rickards 1973). The nearest flattened dimensions to those of the triserial form are those of *T. ensiformis minor* (Mu & Lee 1958), as Fortey (1971) noted, and *P. minor* is used as a specific name here. The obvious disadvantage in using specific nomenclature based on flattened specimens is that no apertural characters are known in such forms. We prefer, nonetheless, to use established names rather than propose a 'parallel' nomenclature for species known from relief or isolated material. We consider that Rickards' wide view of *P. ensiformis* was incorrect and that there are at least two, and possibly more, species in *Pseudotrigonograptus.* Flattened or unflattened this curious and aberrant graptolite is of considerable stratigraphical use.

Pseudotrigonograptus ensiformis (Hall 1865)
Fig. 53a–d

Synonymy in Rickards (1973), excluding the triserial forms included in *P. minor* below.

STRATIGRAPHIC RANGE. Upper part of Olenidsletta Member, V_2b, 102–103 m from base of Member, just below earliest *Isograptus victoriae victoriae* assemblages, and probably base of Castlemainian Ca_2 (= base of *D. hirundo* Zone).

MATERIAL. PMO NF74, NF1493a, NF3389.

DISCUSSION. Two specimens in relief clearly show the quadriserial, scandent nature of this species. The same habit was deduced from topotype specimens of *P. ensiformis* from Quebec described by Rickards (1973), and because our material agrees in other characters the Spitsbergen form is placed in the same species. The broader of our two relief specimens measures 3 mm across the trace of the median septum indicating that this species can be stouter than *P. minor*. The other specimen is 2·3 mm across, which is within the range of variation of the triserial form. Rickards noted that the cross section of this species was an ellipse, rather than circular, and that the shorter diameter of the median septum therefore probably belongs to the shorter axis of cross section. Unlike the topotype specimens ours show some well-preserved thecal apertures (Fig. 53a) which like the triserial species are quite deeply excavated with broad, spoon-like lips. Thecae protrude only about 1·1 mm from the area of common contact with the adjacent thecal series, so that the whole rhabdosome is very compact, and quite unlike *Pseudophyllograptus* in its organization. This leads us to the reconstruction of the cross section of *P. ensiformis* shown in Fig. 53d. Thecal spacing is 10–11 in 10 mm distally. Neither of our specimens is complete: the larger of the two is almost 2 cm long, and was certainly longer when complete, supporting the observation that *P. ensiformis* grew to a larger overall size than *P. minor*.

Mu & Lee (1958) placed *Pseudotrigonograptus* in the family Phyllograptidae. *Pseudotrigonograptus* exhibits none of the proximal end characters typical of the Phyllograptidae, as revised in this work (p. 273; *Phyllograptus, Xiphograptus* gen. nov.). Fortey (1971) showed that the triserial form has an initial development of normal isograptid type. Its affinities more probably lie with *Isograptus* and the Dichograptidae, rather than with *Phyllograptus.* Despite the similarity in habit there is nothing to suggest that *Pseudophyllograptus* is particulary close to *Pseudotrigonograptus,* although both are typically dichograptid in development, and we consider it possible that these genera had independent origins from tetragraptid ancestors. There is no stratigraphical evidence relevant to the origins of *Pseudotrigonograptus*: it appears suddenly and cryptogenetically late in the Arenig, and extends through the Llanvirn. This is a long range, and it would be surprising if the single species *P. ensiformis* were the only one through this time interval. However, the difficulties of recognizing true specific characters from the trace of the median septum alone leads us, like Rickards (1973), to take a very wide view of the species with quadriserial, scandent habit.

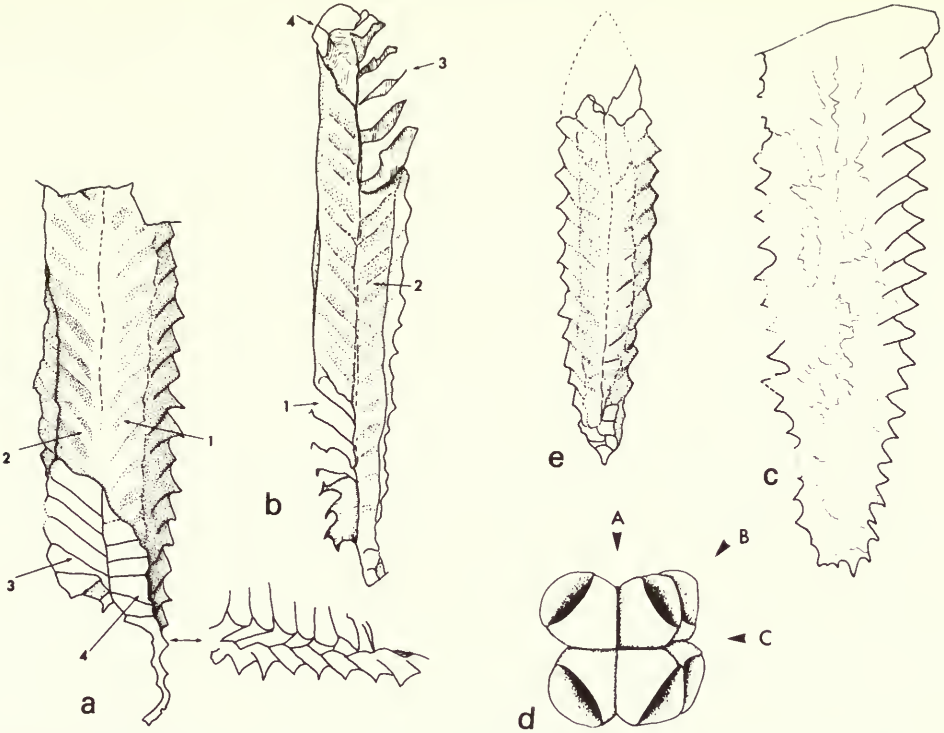


Fig. 53a–c *Pseudotrigonograptus ensiformis* (Hall). a, PMO NF1493a, specimen preserved in full relief, showing the four series of thecae (1–4) and thecal apertures. This is the wide *'Trigonograptus'* mode of preservation shown in Fig. 53d(C). Detail on right shows the lateral view of thecal series 1 and 4 at lower end of stipe. 103 m from base of Olenidsletta Member. b, NF74, showing narrow *'Trigonograptus'* mode of preservation, as in Fig. 53d(A); thecal series 1–4 indicated. 102 m above base of Olenidsletta Member on Profilstranda. c, NF3389, flattened in shale, preserved in 'apertural' aspect as in Fig. 53d(B). Note short interthecal septa unlike *Pseudophyllograptus*; broad belt of periderm in centre may represent crushed, upper, thecal series. Same horizon as b. All × 4.

Fig. 53d Reconstructed cross section of four-stiped *Pseudotrigonograptus*. Flattening, or splitting, in the three directions indicated account for the three preservation modes shown in the series, Fig. 53a–c above; A and C result in splitting along the median 'septum' (short and long respectively) and B results in the apparently biserial mode, with maximum width and full thecal profiles.

Fig. 53e *Pseudotrigonograptus minor* (Mu & Lee). PMO NF3388, typical specimen preserved in relief, with third thecal series removed to show median 'septum' (120° angle between two remaining series). 107 m above base of Olenidsletta Member; × 4.

Flattened specimens found in a shaly bedding plane at the same horizon as relief *P. ensiformis* are certainly referable to this species. It might be possible to mistake them for *Phyllograptus* or *Pseudophyllograptus,* but their identity is betrayed by the very short length of the interthecal septa, with a broad, undifferentiated 'axis', and the low inclination of the thecae (distal inclination of phyllograptoids is always at right angles to the axis of the stipe). If our view of the cross section is correct this flattened material showing the apertures in equal profile should result from flattening in the 'phyllograptoid' mode, with one pair of thecal series normal to the bedding plane, so that the rhabdosome does not get the chance to split along the median septum, as in the usual preservation (Fig. 53d – 'B'). These specimens are 5 mm broad: forms with similar dimensions were described by Cooper (1979: 93) as 'graptoloid genus 1 sp. 3'.

Pseudotrigonograptus minor (Mu & Lee 1958)

Fig. 53e; Pl. 5, fig. 13

1953 *Glyptograptus* aff. *dentatus* (Brogniart); Spjeldnaes: 180; pl. 1, figs 12, 13.
1953 *Glossograptus* aff. *acanthus* Elles & Wood; Spjeldnaes: 181; pl. 1, fig. 7.
1958 *Trigonograptus ensiformis* var. *minor* Mu & Lee: 396, text-fig. 3.
1971 *Tristichograptus ensiformis* (Hall); Fortey: 188–199; pls 26–29; text-figs 1–5.
1979 Graptoloid gen. 1 sp. 1; sp. 2; Cooper: 93; pl. 19d, f; text-fig. 84a.

STRATIGAPHIC RANGE. Upper part of Olenidsletta Member, V_2b–V_3, 102 m to top, and in basal bed of Profilbekken Member. Late Arenig, Castlemainian (Ca_2 to Ca_3), and probably *D. hirundo* Zone equivalent.

MATERIAL. Full range of the material is given in Fortey (1971). PMO NF3385, NF3388 are additionally figured here.

DISCUSSION. This species was described at length by Fortey (1971) from superb isolated material, and repetition is unnecessary here. Cooper (1979) found flattened specimens which show that thecal apertures can be displayed if the graptolite is compressed *in toto*. The more usual mode of preservation is that illustrated in Fortey (1971: text-figs 1c, 2) where the rhabdosome splits along the median septum to present that aspect which lacks apertures. Because the cross section of *P. minor* is nearly circular there is no strongly preferred orientation in flattened material. Two series of apertures are usually visible, but if the boundary wall between the thecae is presented on one side, then the effect is to produce a puzzling-looking graptoloid with only one series of thecal apertures visible (e.g. Cooper 1979: pl. 19d, specimen on right). These flattening properties are explained by the triserial nature of the rhabdosome. Similar properties are shown by the specimens figured by Spjeldnaes (1953) from the *D. hirundo* Zone of Norway, which were wrongly interpreted by him as biserial, scandent forms.

Triserial rhabdosome habit characterizes whole populations; it seems to be a reliable specific characteristic for this reason. Which of a number of specific names proposed by Mu & Lee (1958) to apply to it is more difficult. The width across the median septum presented in the usual mode of preservation is variable, but most specimens are close to 2 mm across any two series of thecae, and the mean value for our population is 2·3 mm. Although the largest specimens are about 2 cm long (e.g. Fortey 1971: pl. 29, fig. 3a) the mean value is 1·5 cm. These proportions are within the range of *Trigonograptus ensiformis* var. *minor* Mu & Lee (1958), and this name seems to be the best available to describe the triserial *Pseudotrigonograptus,* although nothing like the same thecal detail is known from the Chinese material, which is from the *Didymograptus hirundo* Zone of the Ningkuo Shale. Relief material is readily distinguished from the quadriserial species because the angle between adjacent thecal series is 120° , whereas the median septa on the latter intersect at 180°.

Subfamily **ISOGRAPTINAE** Harris, 1933

DIAGNOSIS. Sicula and proximal thecae relatively long; development of isograptid type, dextral or rarely sinistral, sicula and th1[1] symmetrically developed (isograptid symmetry); single dichotomy produces two reclined to scandent stipes, united (biserial) in some scandent forms; thecal inclination initially low or high, distally generally high.

DISCUSSION. Harris's (1933) concept of the Family Isograptidae incorporates the genera *Isograptus* Moberg 1892, *Pseudisograptus* Beavis 1972, *Oncograptus* T. S. Hall 1914, *Cardiograptus* Harris & Keble, *in* Harris 1916, *Skiagraptus* Harris 1933 and *Maeandrograptus* Moberg 1892. His phyletic scheme linking these genera has been revised by Cooper (1973) on the basis of a population study of the group. The *I. victoriae* lineage is regarded as ancestral to both the group with *I. caduceus* and related forms including *Skiagraptus* (*sensu* Harris 1933, *non* Whittington & Rickards 1969), and the *Pseudisograptus* group. There is thus a good phylogenetic basis for distinguishing the group at subfamily level. All members of the plexus possess isograptid symmetry.

The phyletic position of *Oncograptus* and *Cardiograptus* is less certain; they both possess isograptid symmetry and, as Harris pointed out, many other isograptid features but intermediate forms are lacking. In particular the inclusion of *Oncograptus* must remain provisional in view of its apparently anomalous development (Bulman 1936*b*). *Maeandrograptus* (*sensu* Cooper 1973: 57) is excluded from the group and from the subfamily on the grounds that it lacks isograptid proximal symmetry.

The earliest Australasian isograptid, *Isograptus primulus* Harris, appears in the Chewtonian, immediately before the 'burst' of isograptids of the *I. victoriae* lineage in the Castlemainian. Harris regarded *I. primulus* as ancestal to *I. victoriae lunatus* and hence as the progenitor of all later Australasian isograptids. However, there are no transitional populations linking *primulus* and *lunatus* and Cooper (1973) has shown that the changes in passing from *primulus* to *lunatus* (the earliest member of the *victoriae* lineage) have no continuity with the changes involved in the transition from *lunatus* to *victoriae* and later forms. *I. victoriae lunatus* was suggested to have been derived from a reclined didymograptid ancestor by the acquisition of isograptid symmetry, whereas the earlier *I. primulus* was not thought to be closely related to the *victoriae* group and its descendents. Its closest ally was suggested to be the Swedish *I. gibberulus* of Bulman (1932), to which should now be added *I. scandens* sp. nov. from Spitsbergen. *I. victoriae lunatus* and the *I. primulus* group thus do not share an immediate common ancestor and belong to distinctly different lineages. Evolution of the isograptid rhabdosome probably occurred twice.

A phyletically-based classification would thus require two separate major groups. The first would include *I. primulus, I. scandens* and the Swedish *I. gibberulus,* and the second would comprise *I. victoriae* and its descendents including *Pseudisograptus, Skiagraptus* and, provisionally, *Apiograptus* Cooper & McLaurin 1974, *Kalpinograptus* Qiao 1977, *Apoglossograptus* Finney 1978 (*nom. nud.*; probably = *Kalpinograptus*) and *Exigraptus* Mu, *in* Mu *et al.* 1979 (with secondary loss of isograptid symmetry?). Furthermore the two groups could not be embraced by the one subfamily since they are inferred to have been independently derived from dichograptoid ancestors. This means that if a family-group name is maintained for the *I. victoriae–caduceus–Pseudisograptus* plexus then a new genus and subfamily name is needed for the *'I.' primulus* group.

The concept of isograptid development was based on the Swedish *I. gibberulus* (*sensu* Bulman 1932), i.e. on the *primulus* group. However, it is now clear that *both* groups possess isograptid development and symmetry and it is immaterial, for the appropriateness of the term isograptid development, to which group the name *Isograptus* (and Isograptinae) should eventually apply. The two groups represent an example of parallel evolution, a phenomenon that we suspect is commonplace among dichograptoids. The one character that serves to distinguish between the two is thecal inclination; in the *primulus* group thecae throughout the rhabdosome are inclined at a high angle to the dorsal stipe margin from their origins to their apertures whereas in the *victoriae* group all thecae beyond those of the proximal region commence their growth at a low angle to the dorsal stipe margin but curve around to achieve high inclination only in the apertural region.

The next question that arises is, to which of the two groups does Nicholson's (1875) *Didymograptus gibberulus,* the type species of the genus *Isograptus,* belong? Little can be determined from Nicholson's (1875: pl. 7, figs 3, 3a–b) and Elles & Wood's (1902: text-fig. 33a–b; pl. 2, figs 9b, d) figures of the type specimens except that they are unlikely to represent the same species as Holm's material figured by Bulman (1932: pl. 8, figs 1–5). Their relationship to the two groups cannot be determined until the type specimens have been redescribed and a lectotype designated. From his re-examination of the type specimens C. J. Jenkins (personal communication) has concluded that at least two species are represented. It is clearly unwise to formalize the two groups at this stage.

The Subfamily Isograptinae Harris is therefore provisionally retained here for the diphyletic grouping of all the 'isograptid' genera listed above. Isograptid proximal symmetry is a character of the group but is *not* a synapomorphy for the group. It has been acquired independently at least twice.

Genus *ISOGRAPTUS* Moberg, 1892

DIAGNOSIS. Reclined to scandent biramous graptoloids with isograptid development and symmetry.

TYPE SPECIES. *Didymograptus gibberulus* Nicholson 1875.

DISCUSSION. From the foregoing discussion of the Subfamily Isograptinae it is clear that the genus *Isograptus* needs redefinition. It is used here in its diphyletic sense to include reclined biramous dichograptoids with isograptid symmetry.

Representatives of each of the two groups are present in the Spitsbergen succession. The *primulus* group is represented by *I. scandens* sp. nov. which is found in the *D. protobifidus* Zone (Chewtonian), and the *victoriae–caduceus* plexus is represented by *I. victoriae victoriae, I. v. maximus,* and *I. caduceus imitatus,* in Castlemainian beds.

Only one horizon – the 110 m level with *I. v. victoriae* – has a reasonably large sample population and it is not possible to analyse the Spitsbergen isograptids from the point of view of population systematics for comparison with the Australasian populations (Cooper 1973). In terms of the populations approach, the various subspecies are regarded as successive populations with wide, overlapping, ranges of variability. This means that one often cannot assign a solitary specimen to a particular subspecies because it lies in the overlap zone of two successive subspecies. However, if several specimens from a single locality are available, a much greater degree of precision in identification is available. The morphotype approach (Harris 1933; Beavis & Beavis 1974), on the other hand envisages the subspecies as having a non-overlapping range of morphological variation, but overlapping stratigraphical ranges. We prefer the populations approach because it is consistent with the biological concept of species.

Isograptus caduceus imitatus Harris 1933

Fig. 54a–d

1933 *Isograptus caduceus* var. *imitata* Harris: 92, figs 55–59.
1973 *Isograptus caduceus imitatus* Harris; Cooper: 71–74, text-figs 14a–i.
1976 *Isograptus* aff. *caduceus imitatus* Harris; Fortey: 278, text-fig. 7.

STRATIGRAPHIC RANGE. Upper Olenidsletta Member V_3, and basal beds of Profilbekken Member, 125–145 m above base of Olenidsletta Member, upper Castlemainian.

MATERIAL. PMO NF1739 (flattened); NF3332–3, SMA 109734–5 and several other specimens (in full relief).

DESCRIPTION. Rhabdosome is V-shaped rather than U-shaped, the dorsal stipe margins flexing sharply upwards rather than smoothly as in *I. victoriae victoriae.* The sicula ranges from 3·4 to 4·2 mm in length and is about 0·7 mm wide at the aperture. The ventral notch between the free ventral walls of the sicula and theca 1^1 is, in most specimens, narrower and deeper than in *I. victoriae victoriae.* The outline of the ventral margin is deeper in the proximal region than it is in *I. victoriae victoriae,* resulting from the ventrally extended sicula and proximal thecae. This feature is most marked in the specimen from the 125 m level (Fig. 54a) in which the ventral margins of the sicula and first theca project outwards in prominent ventral processes. The specimen is preserved as a flattened rhabdosome in black calcareous shale, in contrast to specimens from the 128–129 m level which are preserved in full relief in limestone. In the absence of an adequate population from the 125 m level it is not possible to assess the significance of this difference except to point out that the feature is one that is unlikely to be greatly enhanced by the flattening process.

The stipes are widest at their origin and gradually taper throughout their length. Proximal stipe width ranges from 2·1–2·3 mm, and maximum stipe length observed is 8 mm. Pendent thecae number 6–8. Thecae midway along the length of the stipe are inclined initially at about 30°; they curve strongly so that their free ventral walls are inclined at about 110°.

DEVELOPMENT. Details of the proximal region can be clearly seen in a few specimens from the 128–129 m level. In most specimens (Fig. 54b) proximal development follows closely that

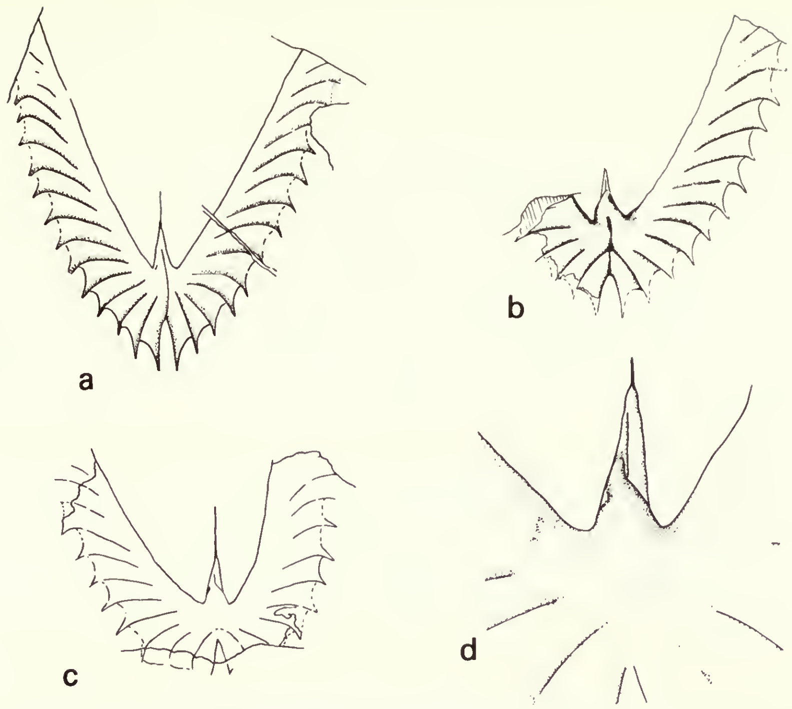


Fig. 54 *Isograptus caduceus imitatus* Harris. a, PMO NF1739, specimen with pronounced V-shape, flattened, resembling lectotype, from 125 m level, Olenidsletta Member, southern section; × 5. b, NF3333, specimen in relief in limestone clearly showing dextral development mode (isograptid type) and an apparent median furrow between th1^2 and th2^1. 128–9 m level, Olenidsletta Member, type section; × 5. c, d, NF3332, specimen in relief (× 5) and enlarged (× 15) proximal region, clearly showing sinistral development mode. Same horizon as b.

described in *I. victoriae victoriae* with th1^2 and th2^1 growing downwards and expanding to form a manubrium-like structure before flexing sharply to commence upward growth. Theca 1^1 originates near the apex of the sicula and th1^2 at about 0·7 mm below the sicula apex. In the specimen shown in Fig. 54b a median furrow separating th1^2 from th2^1 extends upwards from the isograptid arch; it possibly indicates the presence of an internal septum between the two thecae, in which case the crossing canal is restricted to a small opening near the dorsal margins of the two thecae.

Development type and mode were determined in two specimens. In the first it is of dextral mode and isograptid type (Fig. 54b). In the second (Fig. 54c), however, development mode is clearly seen to be sinistral; in all other respects it resembles the normal dextral development. The relative frequency of sinistral development is unknown. Both specimens are from the 128–129 m level.

Discussion. The specimen (Fig. 54a) from the 125 m level matches the lectotype (Cooper 1973: text-fig. 14i) reasonably well, whereas those from the 128–129 m level, with more rounded ventral outlines in the proximal region, best match New Zealand specimens from the upper Castlemainian. The Spitsbergen material from the two horizons, together with the incomplete specimen (Fortey 1976: text-fig. 7) from the basal Profilbekken Member, are all here referred to *I. caduceus imitatus*. Those specimens of the preceding *I. victoriae victoriae* in the Spitsbergen sequence with somewhat V-shaped outlines and projecting sicula and th1^1 (Fig. 55b) closely resemble members of *I. caduceus imitatus*, such as that figured in Fig. 54b, with relatively rounded ventral margins consistent with the inferred derivation of the *caduceus* group from the *victoriae* lineage (Cooper 1973). What is surprising in the Spitsbergen succession is that the one specimen from the 125 m level (Fig. 54a) is more like the later (upper Ca_3 and Ya_1) Australasian *imitatus* than are specimens from the overlying 128–129 m level (Figs 54b–d).

The discovery of a specimen with sinistral development is intriguing. Alternative sinistral and dextral development has been reported in *Tetragraptus serra* by Bulman (1936*a*) and in the dendroids *Dictyonema flabelliforme, Clonograptus tenellus* and *Adelograptus hunnebergensis* by Stubblefield (1929); in all of these species dextral development predominates over sinistral (see Hutt's (1974) comments on *C. tenellus* and *A. hunnebergensis*). Specimens with sinistral development appear to be identical with their dextral counterparts in the same bedding planes in all other respects and there seems no reason to suspect that they were not part of the same population. This would imply that they are polymorphic variants and that the astogenetic rhabdosome development programme of an individual colony can be switched from dextral to sinistral without seriously affecting other aspects of development, at least for those species listed above.

The discovery of sinistral development in an isograptid also goes some way towards resolving the problem of deriving the *Oncograptus* rhabdosome from an isograptid ancestor as suggested by Harris (1933). Bulman's (1936*b*) study of *Oncograptus* showed it to be distinguished from isograptids (and from most dichograptids) in three ways: sinistral development mode, *artus* development type, and possession of an 'extra' theca ($th2^1b$). Sinistral development would not necessarily now imply preclusion of an isograptid ancestor but the two other objections remain.

Isograptus victoriae victoriae Harris 1933

Fig. 55a, b; Pl. 5, fig. 10

1933 *Isograptus caduceus* var. *victoriae* Harris: 90, figs 7–10.
1973 *Isograptus victoriae victoriae* Harris; Cooper: 62–63, text-figs. 9a–f.
1976 *Isograptus victoriae victoriae* Harris; Fortey: 276–277; text-figs 5a–c.

STRATIGRAPHIC RANGE. Upper Olenidsletta Member, V_3, 107–110 m above base, Castlemainian.

MATERIAL. NF1634, NF1647, NF3047 and more than 20 other specimens. All are preserved in full relief in limestone but, unfortunately, disintegrate when isolated by acid solution.

DESCRIPTION. The rhabdosome is U-shaped, the dorsal stipe margins of most specimens curving smoothly away and upwards from the sicular 'wedge'. The stipes reach about 10 mm in

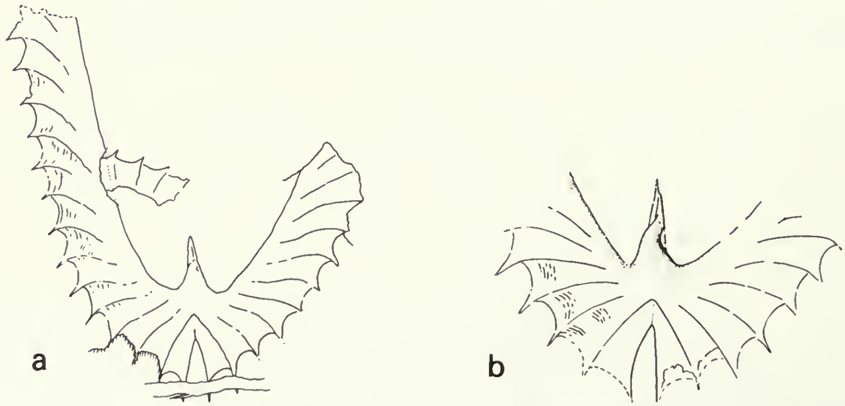


Fig. 55 *Isograptus victoriae victoriae* Harris, rhabdosomes preserved in relief in limestone. a, PMO NF1647, incomplete mature rhabdosome in which proximal thecae have slightly sigmoidal curvature; × 5. b, NF3331, proximal portion showing isograptid, dextral, development; × 6·5. Both from 110 m above base of Olenidsletta Member, type section.

length. The sicula ranges from 3·3 to 4·1 mm (mean value 3·6 mm) in length, and is about 0·7 mm wide at the aperture. The ventral 'notch' between the free ventral margins of the sicula and first theca is relatively narrow and deep and, in a few specimens, is partially filled in by a film of periderm (Fortey 1976: 277). There are 5–7 pendent thecae (*sensu* Cooper 1973).

The sicula and first theca protrude ventrally slightly more than in their Australasian counterparts which have a more rounded ventral rhabdosome margin in the proximal region. Otherwise general rhabdosome shape matches well with the Australasian material.

Stipes are parallel-sided or taper very slightly. Stipe width in the proximal region ranges from 1·9–2·5 mm (mean 2·17 mm). Thecal curvature agrees well with that in Australasian forms except for slight recurvature (particularly in the proximal region) resulting from the initial direction of thecal growth being lateral rather than strictly towards the ventral rhabdosome margin (Fortey 1976: 277). Frequency distributions of sicula length, number of pendent thecae and proximal stipe width are shown in Fig. 56.

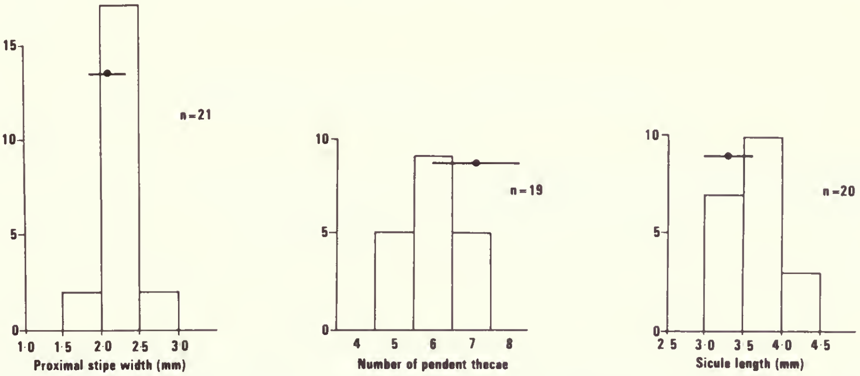


Fig. 56 *Isograptus victoriae victoriae* Harris. Frequency distribution of proximal stipe width and sicula length (taken to nearest whole number) and number of pendent thecae in the population of *I. victoriae victoriae* from the 110 m level in the Olenidsletta Member. The mean value and one standard deviation from the mean for equivalent Australasian samples (from Cooper 1973: 62) is shown for each character.

DEVELOPMENT. Development type and mode can be clearly seen in eight specimens from the external morphology of the proximal region (Fig. 55a). The point of origin of th1^1 lies very high on the ventral side of the sicula. Theca 1^2 originates from th1^1 about 0·75 mm below the apex of the sicula, that is about 0·85 mm above the level at which the dorsal stipe margins diverge from the sicular 'wedge'. It rapidly swells into a conspicuous bulge and expands laterally to mask the sicula and th1^1 completely, as observed from the reverse side of the rhabdosome. Theca 2^1 arises from th1^2 *via* an apparently broad 'crossing canal'. Development in all eight specimens is thus of isograptid type and of dextral mode, as in the Swedish *I. gibberulus* (Bulman 1932: 23–25).

The origin of the stipes (i.e. origins of th1^2 and th2^1) is rather higher on th1^1 than was previously inferred (Cooper 1973: text-fig. 4) in the flattened Australasian material, giving the stipes a greater initial downward component of growth. It is also clear from the Spitsbergen specimens that the base of the supradorsal sicular 'wedge' is broadened by the proximal portions of thecae 1^2 and 2^1, a feature that becomes greatly exaggerated in the manubriate species *(Pseudisograptus),* thought to have been derived from the *victoriae* lineage at about the *maximus* level.

DISCUSSION. The frequency distributions of sicula length, number of pendent thecae and proximal stipe width match well with the mean value and one standard deviation from the mean of the Australasian populations (Fig. 56).

The well-preserved Spitsbergen material shows several details of morphology and development not seen in the Australasian material, all of which is flattened. The subspecies is the first of the *I. victoriae* lineage to appear in the Spitsbergen section, and is found in great abundance at the 110 m level. The slightly deepened ventral rhabdosome margin in the proximal region (rather than a smoothly rounded margin as in Australasian *victoriae*) is a feature which becomes prominent in the *Isograptus caduceus* lineage, suggesting that the Spitsbergen population may be displaced towards the *caduceus* end of the *victoriae* spectrum. Although separation of the *caduceus* lineage does not appear to become complete until the Castlemainian (about *maximodivergens* level, judged from the Australasian sequence) Australasian populations of the earlier forms, *lunatus, victoriae* and *maximus,* contain end members with 'V-shaped' rhabdosomes which were taken as evidence supporting the *victoriae* origin of the *caduceus* lineage (Cooper 1973: 104). The Spitsbergen populations from both the 110 m level *(victoriae)* and 125–129 m level *(imitatus)* provide further supporting evidence and suggest that some degree of geographic isolation may have been involved in the splitting (cladogenesis) event. Relationship of *victoriae* and *imitatus* in the Spitsbergen sequence is discussed under *imitatus*.

Isograptus victoriae maximus Harris 1933
Fig. 57

1933 *Isograptus caduceus* var. *maxima* Harris: 91, fig. 13.
1973 *Isograptus victoriae maximus* Harris; Cooper: 63–65, text-figs 10a–e.
1976 *Isograptus victoriae maximus* Harris; Fortey: 277, text-fig. 6a–b.

Stratigraphic range. Upper beds of the Olenidsletta Member, from 130 m above base to top, and basal bed of the Profilbekken Member.

Material. PMO NF1809, and several incomplete specimens.

Discussion. The figured specimen was noted by Fortey (1976: 277) to match the Australasian modal forms well. Sicula length is 4·5 mm, proximal stipe width is 2·8 mm, distal stipe width is 3·5 mm, and there are about 10–12 pendent thecae. Secondary periderm has been deposited in the apex of the ventral indentation between the sicula and first theca and in the axial region on either side of the sicular 'wedge'. Development details cannot be seen as the specimen is preserved in obverse view, but proximal structure is consistent with an isograptid development type.

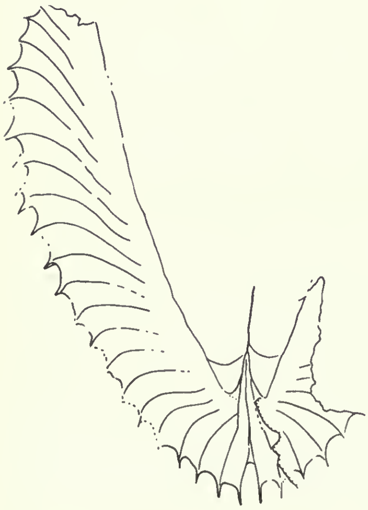


Fig. 57 *Isograptus victoriae maximus* Harris, PMO NF1809, obverse view of incomplete mature rhabdosome; right-hand stipe preserved as impression only. Specimen preserved in relief in limestone, figured by Fortey (1974: text-fig. 6a, b). Basal bed of Profilbekken Member, 145 m above base of Olenidsletta Member; × 4.

With only a single specimen, we cannot rule out the possibility that we have an end member of the *I. victoriae maximodivergens* population instead of *maximus,* since Australasian populations of the two subspecies show considerable overlap (Cooper 1973). However, because the dimensions for sicula length, proximal stipe width and distal stipe width lie so close to the mean values for *I. victoriae maximus,* we refer the Spitsbergen specimen to that subspecies.

Isograptus scandens sp. nov.

Fig. 58a–g; Pl. 5, figs 1–3

DIAGNOSIS. Early *Isograptus* with highly reclined to scandent stipes and highly inclined thecae throughout rhabdosome.

STRATIGRAPHIC RANGE. Olenidsletta Member, V_1c, 49 m from base.

MATERIAL. **Holotype** PMO NF3334; paratypes, PMO NF3335–9, NF3357, NF3379–80 and many other specimens all preserved as flattened casts in black shale.

NAME. 'Scandent.'

DESCRIPTION. The mature rhabdosome has fully scandent stipes whose dorsal margins lie close together, or, in a few specimens, in contact, resulting in a rhabdosome form like that of *Isograptus forcipiformis* or *Skiagraptus.* Stipes are short – up to about 3 mm long – and the rhabdosome has a distinctive ovate outline. Details of the proximal region are obscure in mature rhabdosomes where the distal portion of the sicula commonly appears to be expanded or otherwise modified. Growth stages (Fig. 58a, e, f) clearly show the isograptid symmetry of the sicula and the $th1^1$, however, and the initial downward growth of proximal thecae. The sicula in the growth stages is 2·75–3·0 mm long and about 0·5 mm wide at the aperture. The supradorsal portion is about 1 mm in length and a short (up to 0·5 mm) nema is present in several specimens. In mature specimens the sicula appears to be slightly longer (3·5 mm) and difficult to distinguish in its distal region from its neighbouring theca (presumably $th1^2$). In one specimen (Fig. 58d) the sicula is short and isograptid symmetry is lost.

In their scandent growth the stipes encroach upon the supradorsal portion of the sicula and $th1^1$ (Fig. 58b, c, g). Unfortunately, the flattened rhabdosomes do not allow these details of

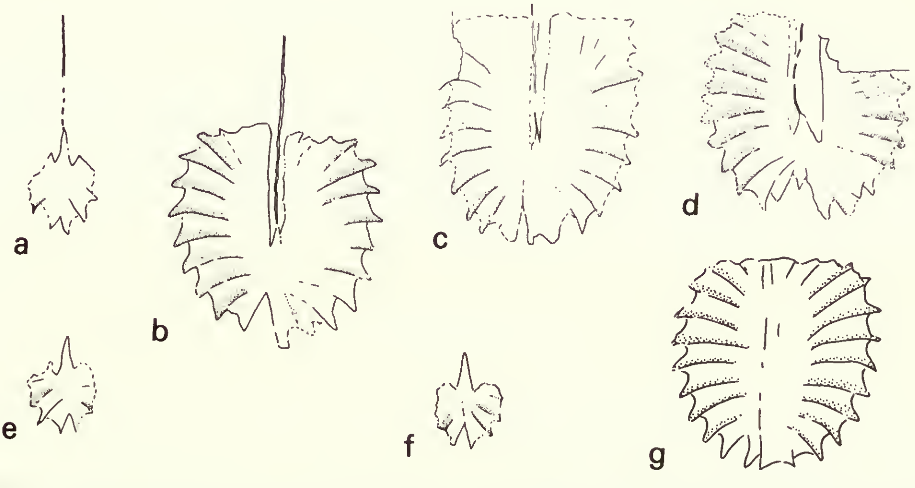


Fig. 58 *Isograptus scandens* sp. nov. All preserved as flattened replaced casts in black shale; all × 5. a, e, f, PMO NF3339, NF3357 and NF3339 respectively; growth stages, showing outline characteristic for growth stages of *Isograptus* species, b, NF3334, **holotype**, best preserved specimen. c, NF3335, large mature rhabdosome, d, NF3336, incomplete mature specimen with sicula possibly inclined and distorted. g, NF3337. All from Olenidsletta Member 49 m above base.

rhabdosome structure to be determined. Stipes reach a maximum width of 2·5 mm in their mid-regions.

Thecae are inclined at a high angle throughout the stipe and are relatively straight. Their ventral margins are commonly enhanced by a thickening of the periderm (i.e. of the replacing mineral) presumably resulting from collapse of the interthecal septum during the flattening of the rhabdosome. There are 8–10 pendent thecae. Thecal apertural margins not deeply recessed.

DISCUSSION. Although most mature rhabdosomes are unmistakably isograptid-like, in several specimens (e.g. Fig. 58d) it is uncertain whether an isograptid or reclined tetragraptid of *T. bigsbyi* type is represented in which the two pairs of stipes are superposed. The distal portion of the sicula is seldom clearly outlined and isograptid symmetry is obscured in some specimens. However, all growth stages show isograptid symmetry and since this feature is not known in any tetragraptid we refer the Spitsbergen form to *Isograptus*. It is assumed that the proximal irregularities affecting the sicula and neighbouring thecae result from either the sicula lying at a somewhat inclined attitude to the median plane of the rhabdosome so as to cause some distortion on flattening or, less probably, that the distal outline of the sicula has been modified by overgrowth (Fig. 58c, g) or resorption (Fig. 58d).

The species is the earliest isograptid in the Spitsbergen sequence where it is confined to the *D. 'protobifidus'* Zone. It is interesting in anticipating the isograptid trend towards scandency; highly reclined or scandent stipes are achieved by other isograptids (e.g. the *manubriatus* and *caduceus* groups) only at much higher stratigraphic levels (Yapeenian). Fusion of the dorsal stipe margins in a specimen such as that of Fig. 58g would result in a rhabdosome of *Skiagraptus* type, at least in outline.

With its highly inclined thecae, the new species differs from all members of the *Isograptus victoriae–caduceus* plexus and instead resembles *Isograptus primulus* Harris from the Chewtonian of Australasia – that is from the equivalent stratigraphical horizon. The Spitsbergen form is distinguished from the Australasian by its scandent stipes. It is thus thought to belong to a group that is phyletically distinct from the *I. victoriae–caduceus* plexus and the acquisition of isograptid symmetry and scandent stipes in the two groups are therefore examples of convergent evolution.

Genus ***PARACARDIOGRAPTUS*** Mu & Lee, 1958

TYPE SPECIES. *Paracardiograptus hsui* Mu & Lee 1958.

REMARKS. *Paracardiograptus* is distinguished by the pronounced outward deflection of several pairs of proximal thecae. The overall shape of the rhabdosome is identical with *Cardiograptus* Harris & Keble (*in* Harris 1916) and unless the interthecal grooves or septa of proximal thecae can be seen, the two genera cannot be distinguished. It is likely that *Paracardiograptus* has sometimes been mistaken for *Cardiograptus* and that distribution of the former is not restricted to China, as appears from the literature.

***Paracardiograptus*? sp.**

Fig. 59

1979 *Paracardiograptus*? sp.; Cooper: 73; pl. 14a, fig. 47.

STRATIGRAPHIC RANGE. Profilbekken Member, V_4b, 65 m above base of member, Yapeenian.

MATERIAL. PMO NF3358.

DESCRIPTION AND DISCUSSION. The single fragmentary specimen is preserved as a carbonized, largely flattened rhabdosome in fine-grained calcarenite. Enough of the rhabdosome is preserved to determine that its outline morphology was most probably that of a *Cardiograptus* such as *C. morsus* Harris & Keble (*in* Harris 1916). Further, traces of an early pair of thecae

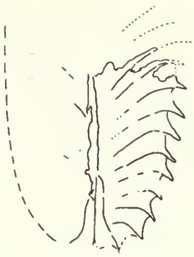


Fig. 59 *Paracardiograptus*? sp. PMO NF3358, fragmentary specimen from Profilbekken Member, V_4b, 65 m above base of member; × 4·5.

(possibly the sicula and th1^1) can be seen to deflect outwards in their distal region. In this feature and in general outline and proportions the specimen matches that from the Yapeenian of New Zealand decribed as *Paracardiograptus*? sp. by Cooper (1979).

The outward deflection of proximal thecae is not known in *Cardiograptus,* but is developed to a marked degree in *Paracardiograptus.* The Nelson and Spitsbergen specimens appear to be intermediate between the two genera. Reference of the Spitsbergen species to *Paracardiograptus* is therefore only tentative.

The chief importance of the Spitsbergen specimen lies in its age implications. Neither *Cardiograptus* nor *Paracardiograptus* are known in rocks older than Yapeenian and both *Paracardiograptus* and *Cardiograptus morsus* are confined to that stage. The Profilbekken Member V_4b interval is therefore taken as Yapeenian in part.

Subfamily **SIGMAGRAPTINAE** nov.

DIAGNOSIS. Sicula relatively long and slender, theca 1^1 originating high on ventral side; first two thecae diverge from sicula more or less at right angles but at different levels, th1^1 above the level of th1^2, giving the proximal region an asymmetrical appearance. Prothecal portion of th2^1 extremely slender. Dichotomies of up to 10 or more orders, terminal stipes from 2 to 20 or more. Dichotomies consecutive or delayed, branching progressive or monoprogressive. Thecae long and slender and of low inclination, stipes slender at least in proximal region. Development isograptid, dextral.

DISCUSSION. The distinctive featues of Sigmagraptinae are the slender sicula and initial thecae, the uneven levels of divergence from the sicula of th1^1 and th1^2 and the extremely slender prothecal portion of th2^1. Thecae throughout the rhabdosome are generally slender, giving the rhabdosome a gracile, commonly rather flexuous appearance, although in some forms thecae and stipes may broaden distally, and in others the proximal region may be thickened by secondary cortical tissue.

The slender prothecal portion of th2^1 can only be seen in isolated relief, or semi-relief, material. It is readily obscured by flattening resulting in a proximal outline with what appears to be *artus* type development. Similarly, subsequent dichotomies employ the normal, isograptid, type of division with a slender 'crossing canal' formed by the prothecal portion of the first daughter theca of the dicalycal theca. Thus development and branching type follow the 'standard' for dichograptoids.

BRANCHING. The branching pattern and number of terminal stipes in the rhabdosome varies widely among the genera here included in the Sigmagraptinae. In *Sigmagraptus,* the initial dichotomy is followed by a succession of dichotomies (up to 10 orders or more) each of which produces one stipe that remains unbranched and a second stipe that undergoes further dichotomy (monoprogressive branching). The resulting characteristic branching pattern is further discussed under *Sigmagraptus,* and we may refer to it as the 'sigmagraptid branching plan'. *Goniograptus* (assuming that we are correct in assigning it to the Sigmagraptinae) undergoes two orders of progressive branching before resorting to the sigmagraptid branching plan and is, in effect, a *Sigmagraptus* based on an initial tetragraptid rather than didymograptid plan.

Where one, two or three 'normal', consecutive dichotomies take place the resulting rhabdosome plan conforms with that of the form genera *Didymograptus, Tetragraptus* and *Dichograptus* respectively. There is thus a series of progressive grades parallel to those of the Dichograptinae and, in fact, the three genera above are those into which species with one, two, or three orders of progressive branching have previously been placed. A parallel stipe reduction series has even been proposed (Harris & Thomas 1942) and may well hold true, although supporting stratigraphic data have not yet been described.

However, here the number of terminal stipes is given less stress in phylogeny and classification than the distribution and arrangement of dichotomies (i.e. the branching programme of the rhabdosome), and all the various reduction stages are not given separate names; where generic names are available they have, however, been used. Those sigmagraptimes with delayed, and often irregular, dichotomies are separated as a distinct genus, *Laxograptus,* within which the number of terminal stipes is highly variable, both within and between species.

Table 2 Distribution of branching and dichotomy character states among genera of the Sigmagraptinae.

Dichotomy spacing	Branching type and order		
	1 progressive, then many monoprogressive	2 progressive, then many monoprogressive	Progressive throughout rhabdosome
Consecutive throughout rhabdosome	*Sigmagraptus* *Trichograptus*	*Goniograptus* *Brachiograptus*	—
1 & 2 consecutive, later orders consecutive *or* delayed	—	—	*Etagraptus*
2nd delayed	*Yushanograptus*	—	—
2nd and later orders delayed	—	—	*Laxograptus*
2nd indefinitely delayed	*Acrograptus*		

Genera included. *Sigmagraptus* Ruedemann 1904, *Trichograptus* Nicholson 1876, *Etagraptus* Ruedemann 1904 (emend.), *Acrograptus* Tzaj 1969 (emend.), and *Laxograptus* gen. nov. (p. 269). Provisionally included are *Goniograptus* M'Coy 1876, *Brachiograptus* Harris & Keble 1932, and *Yushanograptus* Chen, Sun & Han 1964.

The nominate genus includes forms which undergo a single order of progressive branching followed immediately by repeated monoprogressive branching with only a single normal theca interposed between dicalycal thecae throughout the rhabdosome. Exactly the same branching pattern is followed by *Trichograptus* Nicholson 1876, which differs only in that the lateral stipes are disposed on one side of the main axis, rather than alternately on either side as in *Sigmagraptus.* Examination of the holotype of *T. fragilis* in the BM(NH) revealed a long slender sicula and slender thecae throughout the rhabdosome, and a proximal outline closely similar to that of *Sigmagraptus.* We doubt that the two should be maintained as distinct genera, in which case *Trichograptus* has priority.

Yushanograptus has a similar branching pattern to that of *Sigmagraptus* but several (about 10) normal thecae are interposed between the first and second dicalycal thecae resulting in a relatively long pair of primary stipes. Its inclusion in the Sigmagraptinae is provisional until details of its proximal structure are clearer.

Goniograptus and *Brachiograptus* each have two orders of progressive branching followed immediately by many orders of monoprogressive branching. The distinction between them is equivalent to the distinction between *Sigmagraptus* and *Trichograptus* mentioned above and the same reservations about their validity as distinct genera apply. They are only provisionally included in the subfamily until details of their siculae and proximal structure are better known.

Where three orders of progressive branching take place, with interposition of only one normal theca between dicalycal thecae (consecutive dichotomies), the result is a rhabdosome of *Dichograptus* plan. Several slender '*Dichograptus*' species have been described that are likely to be sigmagraptines, including *D. tenuissimus* Harris & Thomas 1942. Similarly, where two orders of progressive branching take place in succession (consecutive dichotomies), the result is a rhabdosome of tetragraptid plan. *Etagraptus* Ruedemann 1904 is a sigmagraptine, as pointed out in our discussion of the form genus *Tetragraptus,* with a rhabdosome of tetragraptid plan. Since the name *Etagraptus* is available, it is here used for the entire group of sigmagraptines with two, three or more orders of progressive branching produced by consecutive dichotomies.

Where only a single, initial, dichotomy takes place the result is a rhabdosome of didymograptid plan. The name *Acrograptus* is available and is here used to denote sigmagraptines with didymograptid rhabdosomes.

Where dichotomies, after the first, are delayed to a greater or lesser extent the result is an irregular rhabdosome for which there is no defined dichograptoid genus available. The name *Laxograptus,* based on *Zygograptus irregularis* Harris & Thomas 1941, is here proposed for such forms. Some of the other species of *Zygograptus* described by Harris & Thomas (1941: 308–310; pls 1, 2) have slender rhabdosomes and may also be sigmagraptines, in which case the range of branching patterns would be further extended. However, until the type species, *Z. abnormis* J. Hall, is better known, the genus *Zygograptus* is best excluded from the Sigmagraptinae.

Genus *SIGMAGRAPTUS* Ruedemann, 1904

[= *Hemigoniograptus* Jin 1977: 81]

Type species. *Sigmagraptus praecursor* Ruedemann 1904.

Diagnosis (revised). Sigmagraptines with one order of progressive branching followed by many orders (up to 10 or more) of monoprogressive branching, the undivided stipes lying alternately on opposite sides of a main axis formed by the dicalycal thecae. Dichotomies consecutive throughout rhabdosome. Sicula very long and slender, theca 1^1 originating high on its ventral side. Thecae very slender.

Discussion. The above diagnosis incorporates the new information from the Spitsbergen isolated material. It is now clear that the rhabdosome is essentially half of a *Goniograptus* rhabdosome and apparent anomalies in branching mode have been removed. The term stipe is sometimes used for the main zigzag axes and is convenient but is not strictly correct as they themselves divide at each angulation by a process of normal dichotomous division and each segment should thus be regarded as a separate stipe. Dichotomies thus reach to a high order (10 or more).

The genus contains three species: *S. praecursor* Ruedemann 1904 (= *S. laxus* (T. S. Hall 1914)), *S. crinitus* (T. S. Hall 1914), and *S. yandoitensis* Harris & Thomas 1938. However, it should be noted that if there is more than one theca between branching nodes in *S. yandoitensis* as tentatively suggested by Harris & Thomas, then it would be excluded from the genus *Sigmagraptus* on the above diagnosis. The 'heavy' rhabdosome of *S. crinitus* conflicts with the general rule of slender rhabdosomes in Sigmagraptinae. However, growth stages of *S. crinitus* have not yet been described and it is possible that the thick axial 'stipes' have been produced at a late stage by deposition of secondary cortical tissue as happens in *Clonograptus flexis* (? = *C. rigidus*) described by Braithwaite (1976: 15–19).

Sigmagraptus praecursor Ruedemann 1904
Figs 60a–d, 61a–k

1902 Coenograptid n.gen. n.sp. Ruedemann: 566.
1904 *Sigmagraptus praecursor* Ruedemann: 702–703; pl. 5, fig. 13; text-fig. 93.
1914 *Goniograptus laxus* T. S. Hall: 113, text-fig. 4.
1935 *Sigmagraptus laxus* (T. S. Hall) Benson & Keble: 272–273; pl. 32, figs 10, 11, ?12.
1947 *Sigmagraptus praecursor* Ruedemann; Ruedemann: 300; pl. 49, figs 17–20.
1974 *Sigmagraptus praecursor* Ruedemann; Rickards: 232–239, text-figs 1A–J, 2A–H, 3A–C.
1979 *Sigmagraptus laxus* (T. S. Hall); Cooper: 57; pl. 49; text-fig. 22.

STRATIGRAPHIC RANGE. Olenidsletta Member, 13–21 m above base, V_1b.

MATERIAL. SM A105799–800, A105802–6, isolated flattened specimens; PMO NF2353, NF2392–3, NF2841, NF2853–4 and several other fragmentary specimens preserved in rock.

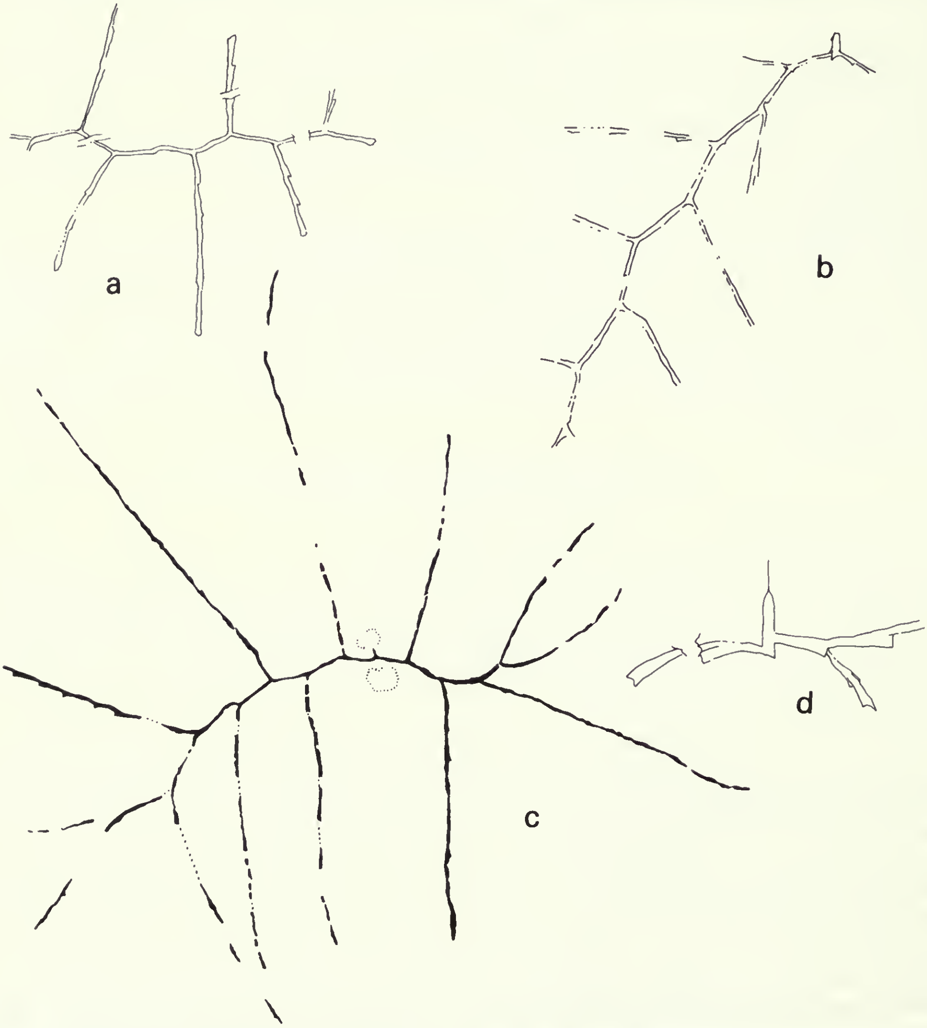


Fig. 60 *Sigmagraptus praecursor* Ruedemann. a, PMO NF2854, incomplete rhabdosome; 18–19 m above base Olenidsletta Member, southern section; × 3. b, NF2393, incomplete mature specimen showing alternate 'lateral' branching; 20–21 m above base Olenidsletta Member, southern section; × 3. c, NYSM 16006, holotype figured by Ruedemann (1904: pl. 5, fig. 13; text-fig. 93), from Bed 3 (*bifidus* Zone) of New York; × 3. d, NF2853, proximal region of specimen in same slab as that of a, showing sigmagraptid asymmetry; × 6.

DESCRIPTION. The rock slab material is fragmentary but sufficient to provide the distinctive features of rhabdosome morphology. Chief interest lies in the isolated material which has yielded several proximal growth stages and branching stipe fragments, and from which initial development and branching mode can be clearly deduced.

Dichotomies up to the 8th order are present in the rock-preserved material and are spaced about 1·8–2 mm in the proximal part of the rhabdosome and 2·2–3 mm in the distal part of the rhabdosome. 'Lateral' stipes reach up to 0·3–0·4 mm in dorsoventral width and some isolated fragments show undulations of the dorsal margin (Fig. 61g, h), not clearly visible in the rock-preserved material. Thecae are spaced approximately 7–9 in 10 mm.

DEVELOPMENT. The sicula is long and slender, measuring 1·1 to 2·0 mm in length and about 0·16–0·19 mm in dorsoventral width at its aperture. The ventral side of the sicula is marked by an extended lip or apertural process. The distal portion of the sicula is deflected towards the stipe^2 side. Theca 1^1 originates high on the ventral side of the sicula (probably the metasicula), grows down beside it and then curves sharply away from it, leaving 0·1–0·2 mm of the sicular ventral wall free. Theca 1^2 is given off immediately before the sharp deflection and grows down and across the sicula before turning outward; its ventral margin is approximately aligned with the dorsal margin of the sicular aperture. The first two thecae thus emerge from the sicula at markedly different levels (Fig. 61c, e), giving a characteristically asymmetrical appearance to the proximal end.

Immediately after its origin, th1^2 gives rise to th2^1 which then grows out as an extremely slender tube along the dorsal side of th1^1. Development is thus of isograptid type and dextral mode. Later development stages were not found.

BRANCHING. An isolated branching stipe fragment (Fig. 61i) shows that the dicalycal theca (n) arises from th(n – 1) at the level of the aperture of the previous theca (n – 2). The dicalycal theca grows away from its parent theca to form one branch and gives off its first daughter theca almost immediately which in turn follows the parent theca (n – 1) to give rise to the second branch. Branching mode is thus of isograptid type. In relating the isolated branching fragment to the rhabdosome, two interpretations are possible. The dicalycal theca may comprise the main zigzag stipe (Fig. 61j) or it may form the basal theca of the lateral branch (Fig. 61k). Because there is no evidence of a second branching node at the level of the aperture of theca (n + 1) as would be expected in the second interpretation above, the first interpretation is favoured here. Of the two it is the one consistent with Rickards' (1974: fig. 2F) figure showing the dicalycal theca producing its daughter theca about halfway between branching nodes as a 'distinct lump'. The dicalycal theca is thus 'free' in its mid region, and the main 'stipe', at this point, is composed of but a single theca. In the alternative view (Fig. 61k) the main stipe is comprised of two adjacent but not successive thecae at any given point. In either case, each dicalycal theca alternates with a normal unicalycal theca.

The interpretation preferred here is consistent with branch structure in *Goniograptus* described by Jaanusson (1965) but conflicts with that described by Rickards (1974; see discussion below) in *Sigmagraptus praecursor*. It also indicates that 'lateral' branch formation does not differ fundamentally from dichotomous stipe division.

OVERALL DEVELOPMENT PLAN. A model for the overall thecal budding plan of the rhabdosome can thus be proposed and is shown in Fig. 62. The main zigzag axes or 'stipes' are composed of dicalycal thecae and the unbranched 'lateral' stipes develop from the first of the two daughter thecae of each dicalycal theca. Throughout the rhabdosome, dichotomies are consecutive and dicalycal thecae are separated, in budding sequence, by a single normal (unicalycal) theca.

DISCUSSION. The species is commonly found in great profusion, forming dense mats on the bedding plane. One specimen (NF2853, Fig. 60d) shows the distinctive asymmetrical proximal end, otherwise known only from isolated material. Length of the sicula is variable in the Spitsbergen material but generally is less than 1·5 mm.

Ruedemann's figures (1904: pl. 5, fig. 13; text-fig. 93) of the holotype from Bed 3 (*bifidus* Zone) of New York show an improbably long sicula, at least 5 mm long. The specimen has

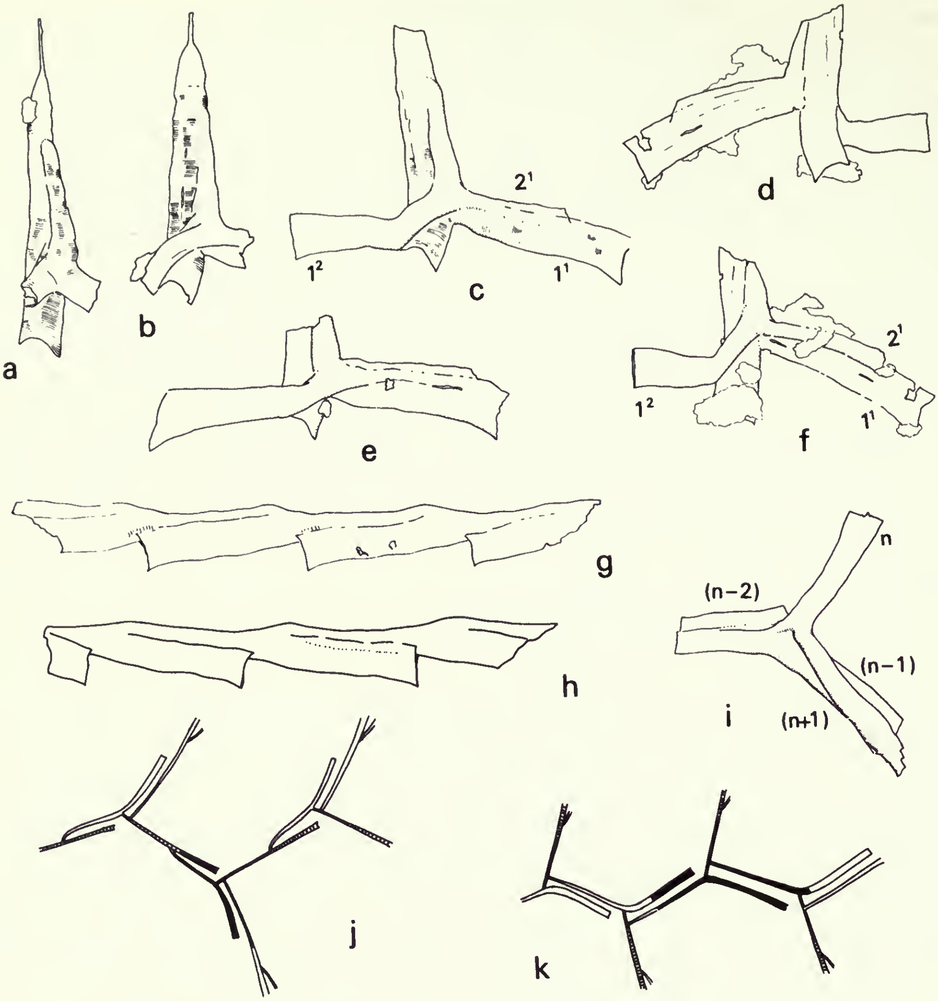


Fig. 61 *Sigmagraptus praecursor* Ruedemann, isolated specimens from Spitsbergen. a, SM A105806, early growth stage showing origin of th1^1 on, probably, metasicula and ventral apertural extension of sicula. From 17–18 m level; × 30. b, SM A105802, incomplete later stage, isograptid arch formed. From 16–17 m level; × 30. c, SM A105800, stage in which th2^1 has grown part way along the dorsal margin of th1^1 as a slender tube, isograptid development clear. From 16–17 m level; × 30. e, SM A105799, incomplete growth stage similar to that of c. From 16–17 m level; × 30. g, h, SM A105805 and SM A105804 respectively, stipe fragments showing weakly-developed prothecal folds. g from 17–18 m level, h from 16–17 m level; × 20. i, SM A105803, fragment of branching stipe from 16–17 m level on which thecal diagrams shown in Fig. 61j (preferred here) and Fig. 61k have been based; × 30. d, f, SM A105807, sigmagraptine growth stage possibly referable to *S. praecursor* in which the sicula protrudes below the level of th1^1 and in which isograptid development is clearly displayed. From 16–17 m level; × 30. All from Olenidsletta Member, type section.

been re-examined and is refigured in Fig. 60c. There is no trace of the structure figured by Ruedemann but the shale matrix has been excavated at two places, one above and one below the median axis of the rhabdosome. The apex of a longer sicula could have been removed by one excavation, but the other lies clear of the ventral rhabdosome margin and there is no sign of a projection of the sicula below the ventral rhabdosome margin as would be expected from

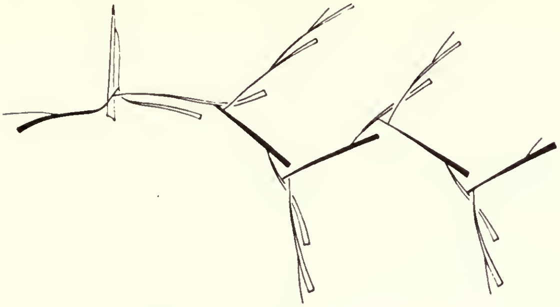


Fig. 62 *Sigmagraptus praecursor* Ruedemann. Thecal diagram to show our inferred overall thecal budding plan of the rhabdosome. Dicalycal thecae shown in solid black. Proximal development is of isograptid type and dextral mode and all subsequent dichotomies employ isograptid division; successive dicalycal thecae are separated by unicalycal thecae.

Ruedemann's figure. It is assumed that the original figure incorporated a misinterpretation of the sicula. The Spitsbergen material matches the refigured holotype and Ruedemann's description well except in having a somewhat wider spacing of dichotomies in the distal part of the rhabdosome.

Rickards (1974) described a population of flattened and pyritized rock-preserved material of *S. praecursor* from the Levis Shales at localities attributed to Zone C. Associated forms include *D. bifidus* (a Zone C form), and *Tetragraptus fruticosus* suggesting that Zone B may also be represented. He interpreted initial development as of *artus* (= '*bifidus*' type). In describing the mode of branching Rickards (1974: 236) interpreted the basal theca of the branch as arising directly from what he interpreted as the dicalycal theca of the 'main stipe'. Branching mode would thus be of *artus* type (and unique) and the 'main stipe' was therefore thought to be composed of a succession of dicalycal thecae with no intervening unicalycal thecae, differing from that of *Goniograptus* (Jaanusson 1965) in which the dicalycal thecae alternate with normal unicalycal thecae.

The isolated Spitsbergen material described here, however, clearly shows that both initial development and branch structure are of isograptid type. Some of the isolated proximal ends, on the other hand, are flattened to the extent that the initial slender part of $th2^1$ cannot be discerned and the 'isograptid arch' is obscured. Such specimens have the appearance of possessing *artus* type development, as drawn by Rickards, but there is little doubt as to their true mode of development and they emphasize the importance of well-preserved material for the interpretation of development and structure of slender dichograptoids. Similarly the intricate isograptid branch structure is apparent only in our well-preserved isolated material. It seems likely that these fine details of structure were not preserved in Rickards' material. No structures equivalent to the peculiar pseudovirgulae described by Rickards are present in our material, but the appropriate growth stages may not be represented.

The form referred by Australasian workers (Benson & Keble 1935; Cooper 1979) to *Sigmagraptus laxus* (T. S. Hall 1914) is here thought to be synonymous with *S. praecursor* Ruedemann. Hall's description is extremely brief but is consistent with Ruedemann's species and his figure shows only generalized rhabdosome form. Hall did not comment on the distinction of *laxus* from *praecursor* and there seems insufficient reason for maintaining it as a distinct species.

Sigmagraptus (?) *crinitus* (T. S. Hall 1914)

Pl. 2, fig. 4

?1914 *Goniograptus crinitus* Hall: 111–112, text-figs 2, 3.

STRATIGRAPHIC RANGE. Lower Olenidsletta Member 13 m from base, in Late Bendigonian (early Arenig) fauna.

MATERIAL. One nearly complete rhabdosome, SM A105819.

DISCUSSION. The determination given here is based on the good specimen of *G. crinitus* from Victoria illustrated by Harris & Thomas (1939: fig. 14); the specimen from Spitsbergen is not well enough preserved to show thecal details. This is a very robust *Sigmagraptus* species compared with *S. praecursor,* which is the common form in our collections. The two zigzag main stipes are much thicker than the laterals, and they appear to curve gently upwards distally. Lateral branches are spaced about 3 mm apart on the same side of each primary stipe; initially they are straight and rigid, but distally they become bent or twisted, suggesting that they were originally quite flexible. Some of these slender laterals certainly exceeded 4 cm in length. *S. crinitus* is a rather distinctive species, and this is its first record outside Bendigo, Victoria.

The sigmagraptine affinity of the species is not apparent from either our material or from the Victorian specimen. Details of proximal structure cannot be seen in specimens from either region, and the nature of the heavily thickened zigzag stipe and arrangement of thecae along it are similarly unknown. Until these details are clarified the species is only provisionally included within the genus.

Genus ***GONIOGRAPTUS*** M'Coy, 1876

TYPE SPECIES. *Didymograpsus thureaui* M'Coy 1876.

Goniograptus thureaui (M'Coy 1876)

Pl. 3, fig. 1

1876 *Didymograpsus thureaui* M'Coy: 128–130, one fig.
1904 *Goniograptus thureaui* (M'Coy); Ruedemann: 621–624, text-figs 37–38; pl. 6, figs 1–15.
1939 *Goniograptus thureaui* (M'Coy); Harris & Thomas: 55, figs 1a–b.
1979 *Goniograptus thureaui* (M'Coy); Cooper: 56; pl. 5d.

STRATIGRAPHIC RANGE. Lower part of the Olenidsletta Member (early Arenig, late Bendigonian); associated trilobite fragments indicate about 4 m from base.

MATERIAL. A single incomplete specimen. SM A105820.

DISCUSSION. The only specimen of this species was found loose on Olenidsletta, but there is no doubt that it came from the lower (Bendigonian) part of the Olenidsletta Member. The proximal end is not preserved, but three of the four stipes are visible, and there is no question of its reference to *Goniograptus.* There appear to have been three or four branches on each side of the four major stipes, and the half rhabdosome preserved suggests that the whole specimen would have had 24–26 branches. This is somewhat less than typical specimens from Bendigo, Victoria (Harris & Thomas 1939) and New Zealand (Cooper 1979). It is like the forms that Ruedemann (1904) termed var. *postremus* and Harris & Thomas (1939) var. *inequalis.* Only two species of *Goniograptus* are like our form: *G. thureaui* and *G. speciosus* T. S. Hall. The latter has much thicker and longer stipes than our specimen, and the proportions, and what thecal details there are, agree closely with descriptions of *D. thureaui* in Ruedemann (1947) and Cooper (1979). The 'varieties' recognized by Harris & Thomas (1939) and Ruedemann (1904) are probably no more than intraspecific varients, with relatively fewer branches.

Genus ***ETAGRAPTUS*** Ruedemann, 1904, emend.

TYPE SPECIES. *Etagraptus lentus* Ruedemann 1904.

DIAGNOSIS (revised). Sigmagraptines with stipes of two, three or more orders in which dichotomies of the first two orders are consecutive. Branching of progressive type.

SPECIES. *Etagraptus lentus* Ruedemann 1904, *Dichograptus tenuissimus* Harris & Thomas 1942, (?) *Bryograptus pusillus* Ruedemann 1904 and (?) *Tetragraptus harti* T. S. Hall 1914.

Discussion. The dicalycal thecae of the first two dichotomies are separated by a single normal theca resulting in an initial development of the rhabdosome following the tetragraptid plan. The third dichotomy, if present, follows the second with one or more intervening normal thecae; in those rhabdosomes with only one intervening normal theca, e.g. in '*Dichograptus*' *tenuissimus,* the rhabdosome plan follows that of *Dichograptus.* In *Bryograptus pusillus* the third and subsequent dichotomies are somewhat delayed. *B. pusillus* departs from a general pattern among sigmagraptines in having pendent rather than horizontal first-order stipes and is therefore only tentatively included here. It seems best, however, to leave the generic diagnosis sufficiently broad to receive such forms.

Ruedemann's (1947: 312) diagnosis of *Etagraptus* incorporated *Tetragraptus approximatus* and laid emphasis on the H-shape of the rhabdosome. We emphasize the sigmagraptine character of the rhabdosome and regard the number and attitude of stipes as of secondary importance.

Several of the Arenig species now usually classified under the 'umbrella-name' *Clonograptus* are likely to belong here.

Etagraptus tenuissimus (Harris & Thomas 1942)

Fig. 63a

1942 *Dichograptus tenuissimus* Harris & Thomas: 366; pl. 1, figs 3, 3a.

Stratigraphic range. Olenidsletta Member, 18–19 m above base, V_1b.

Material. PMO NF2814 and other incomplete rhabdosomes in the same slab.

Description. Rhabdosome of *Dichograptus* grade with three orders of consecutive branching. Sicula morphology and proximal structure unknown. First-order stipes together are 2·4 mm long and appear to be comprised of a single theca each. Second-order stipes are also composed of a single theca each and are 1·0–1·2 mm long. Third-order stipes are at least 6·5 mm long and have a slight dorsal undulation. Stipes of first and second orders are about 0·2 mm in lateral width, those of the third order reach 0·4 mm in dorsoventral width. Thecae are long and slender and inclined at less than 20°. They are spaced 4 in 5 mm (= 8 in 10 mm).

Discussion. Harris & Thomas (1942: 366) claimed that the closest relatives of this slender dichograptoid of *Dichograptus* grade lie not within the genus *Dichograptus* but in other

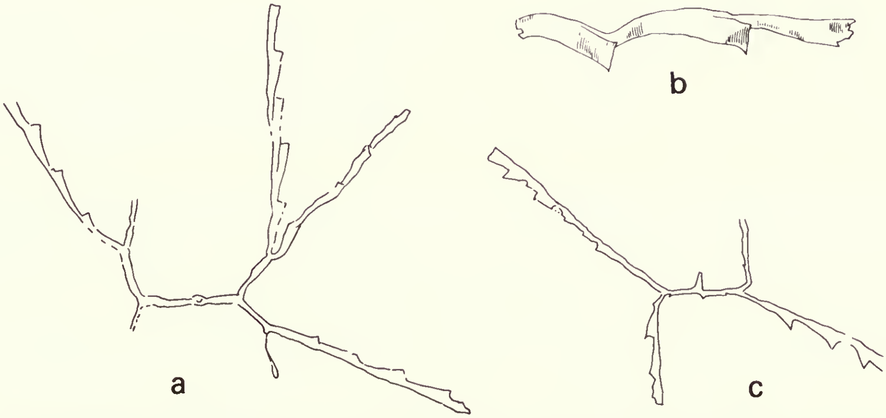


Fig. 63 a, *Etagraptus tenuissimus* (Harris & Thomas), PMO NF2814, incomplete mature rhabdosome from 18–19 m above base of Olenidsletta Member, southern section; × 5. b, SM A105808, fragment of stipe possibly attributable to *E. tenuissimus*, 16–17 m above base of Olenidsletta Member, × 20. c, *Etagraptus* sp. indet., PMO NF2803; incomplete rhabdosome from 25 m above base of Olenidsletta Member, southern section; × 3.

'genera' such as *Goniograptus (G. macer), 'Tetragraptus' (T. harti), 'Didymograptus' (D. gracilis),* etc. In other words they took as a key character thecal type rather than number of stipes (or dichotomies).

Our observations on the admittedly imperfect Spitsbergen material fully support the conclusions of Harris & Thomas. We therefore group this species with other slender species with similar thecae – in the Sigmagraptinae. Unfortunately, sicular morphology and proximal structure are unknown and the assignment must remain provisional.

Etagraptus harti (T. S. Hall 1914)

Fig. 64

1914 *Tetragraptus harti* T. S. Hall: 113–114, text-figs 5–6.
1938 *Tetragraptus harti* Hall; Harris & Thomas: 73; pl. 2, figs 14a–b; pl. 4, fig. 13.
?1964 *Tetragraptus zhejiangensis* Ge: 393–394; pl. 1, figs 1–8.
1979 *Tetragraptus harti* Hall; Cooper: 65; pl. 7f, fig. 33.

STRATIGRAPHIC RANGE. Olenidsletta Member, 18–19 m above base, V_1b.

MATERIAL. PMO NF2854, and several immature rhabdosomes.

DESCRIPTION. Rhabdosome horizontal. Details of sicula and early development unknown. First-order stipes appear to be composed of a single theca each and together form a 'funicle' 2·5 mm long. Second-order stipes are straight, rigidly diverging, and slender reaching a maximum width of 0·5 mm at the 7th theca. Length of second-order stipes reaches 14 mm but isolated stipe fragments possibly attributable to the species are considerably longer. Thecae are of low inclination and in some views appear to be slightly sigmoidal, with a gently undulating dorsal stipe margin. They are spaced 7 in 10 mm (6 in 8·5 mm).

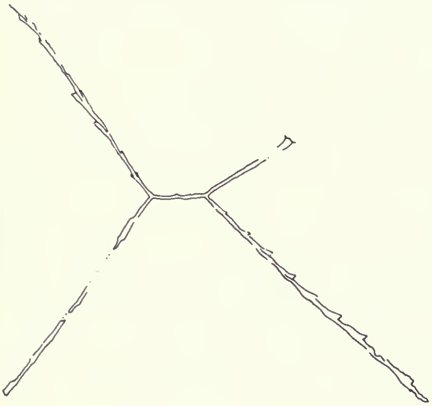


Fig. 64 *Etagraptus harti* (T. S. Hall), PMO NF2854, incomplete mature rhabdosome with second-order stipes showing gentle dorsal undulations; 18–19 m above base of Olenidsletta Member, southern section; × 3.

DISCUSSION. Although only a single specimen has been referred to *E. harti,* the species is likely to be more abundant in our collections. Several bedding planes at about the 18–19 m level are littered with stipe fragments or superposed specimens that are insufficiently clear to be assignable to a species but some of which probably represent *E. harti.*

Hall's species is not particularly well characterized but the Spitsbergen material is obviously similar in gross rhabdosome dimensions and in general thecal characters. Hall's specimens come from the Bendigonian of Victoria, a similar horizon to that of the Spitsbergen specimens.

The species is distinguished from other quadriramous dichograptoids by the extreme tenuity and rigid divergence of its stipes. *Etagraptus lentus* Ruedemann has somewhat lax second-order stipes and the rhabdosome has an H-shape. *Tetragraptus quadribrachiatus* has a similar rhabdosome shape but heavier stipes and more highly inclined thecae. *Tetragraptus zhejiangensis* is closely similar but comes from a considerably higher horizon and appears to have slightly dependent second-order stipes (Ge 1964: pl. 1, figs 5, 6).

Harris & Thomas (1942) have suggested that *E. harti* forms part of a lineage including *Goniograptus macer, 'Dichograptus' tenuissimus* and *'Didymograptus' gracilis*. The slender stipes with widely spaced thecae of low inclination certainly strongly suggest that it belongs (along with the above species) in the Sigmagraptinae. The species is therefore here referred to the genus *Etagraptus* although until details of sicular morphology and proximal structure are known, the assignment must remain provisional.

Genus *LAXOGRAPTUS* nov.

TYPE SPECIES. *Zygograptus irregularis* Harris & Thomas 1941.

DIAGNOSIS. Sigmagraptines with stipes of two or more orders in which dichotomies after the first are delayed and somewhat irregular. Branching is generally of progressive type; rhabdosome of lax habit.

NAME. *Laxus,* 'loose,' referring to the branching habit.

SPECIES. *Zygograptus irregularis* Harris & Thomas 1941, *Bryograptus lapworthi* Ruedemann 1902, *Tetragraptus whitelawi* T. S. Hall 1914, and (?) *Dichograptus sedecimus* Harris & Thomas 1938.

DISCUSSION. The initial dichotomy produces a pair of relatively long first order stipes. It is followed by further dichotomies at delayed and somewhat irregular intervals producing branching of generally progressive type of up to four, five or even more orders. The irregular spacing of dichotomies appears to be variable from one rhabdosome to another, and within single rhabdosomes. In this respect they depart conspicuously from the general rule of regularity and symmetry in rhabdosome development in the Graptoloidea, and recall the irregularity and 'instability' in development of many dendroids, particularly *Adelograptus* and *Bryograptus*.

The first dichotomy and, indeed, the development of the proximal region as far as it can be determined, is of normal sigmagraptine type. The second dichotomy takes place after several thecae of the first-order stipes have been formed. In *L. irregularis* the first-order stipes can be of different lengths (Harris & Thomas 1941: 310) and bear up to 10 or more thecae. The number of thecae in stipes of later orders again is variable within and between specimens. In *L. irregularis* some second-order stipes fail to divide at all. Where dichotomies after the first are relatively closely spaced, the rhabdosome form approaches that of *Zygograptus* Harris & Thomas.

In specimens of *L. irregularis* from New Zealand, figured by Cooper (1979: pl. 3f) the postponement of dichotomy, after the first, is extremely marked. The longer of the two first-order stipes contains at least 21 thecae and second-order stipes contain 16 or more thecae. Incomplete growth stages of these rhabdosomes are indistinguishable from *Acrograptus* which could easily be produced by indefinite delay of the second dichotomy. If dichotomies after the second were indefinitely delayed the result would be a rhabdosome like that of *Tetragraptus whitelawi* T. S. Hall.

The significance of the denticulate apertural extensions in *Dichograptus sedecimus* (Harris & Thomas 1938) is uncertain. Whereas such a thecal character would be expected to carry taxonomic significance at a fairly high level, the feature is shown by several species of different genera from the same locality – the 'Good Bed' of Campbelltown, Victoria – leading to the suggestion that it might be environmentally induced, and hence of limited taxonomic value. The species is therefore tentatively included here.

Some of the Arenig *Clonograptus* species, such as *C. ramulosus* Harris & Thomas 1938 and *C. rarus* Harris & Thomas 1938, with slender flexuous rhabdosomes and delayed branching, might well belong in *Laxograptus*.

Laxograptus irregularis (Harris & Thomas 1941)

Fig. 65a–d; Pl. 4, fig. 1

1941 *Zygograptus irregularis* Harris & Thomas: 310; pl. 1, figs 7–9; pl. 2, fig. 5.
1979 *Zygograptus irregularis* Harris & Thomas; Cooper: 57–58; pl. 3f.

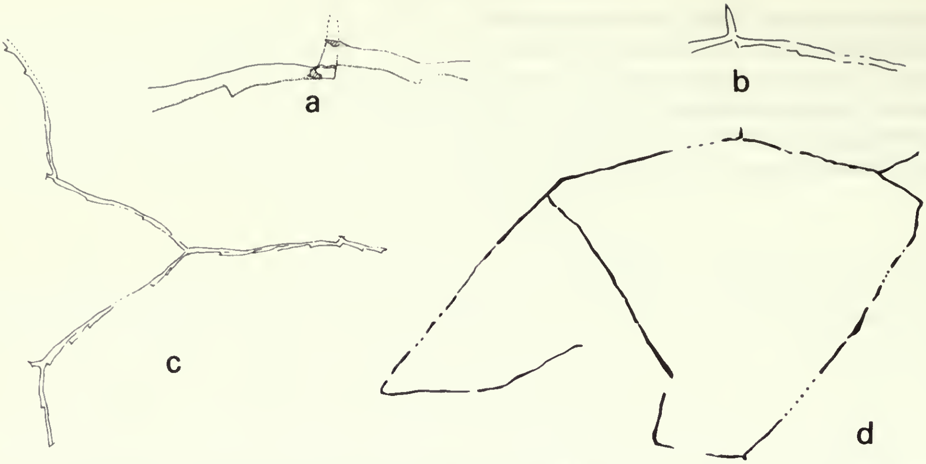


Fig. 65 *Laxograptus irregularis* (Harris & Thomas). a, PMO NF3330a, proximal region showing different levels of divergence of initial two thecae from sicula; 16–17 m above base of Olenidsletta Member, type section; × 12. b, d, NF658, enlarged proximal region (× 5) and incomplete mature rhabdosome (× 2). Note asymmetry in first-order stipe length. 54 m above base of Olenidsletta Member, type section. c, NF3330b, incomplete specimen with 3 orders of dichotomy. Same slab as a; × 4.

Stratigraphic range. Olenidsletta Member, 16–54 m above base, V_1b and V_1c.

Material. PMO NF658 and NF622 (counterparts), NF3330, SM A105807 (?) and numerous fragments.

Description. Rhabdosome of lax habit and at least three orders of slender flexuous stipes. Sicula relatively long and slender, proximal region of sigmagraptine type with the two initial stipes diverging from the sicula at different levels. Proximal development is unknown but the similarity of the proximal outline to that of *Sigmagraptus praecursor* suggests that proximal structure in the two forms is similar. First-order stipes with five or more thecae, varying in length from rhabdosome to rhabdosome; together they form a more or less straight 'funicle'. Second-order stipes with six or more thecae, again varying in length from rhabdosome to rhabdosome. Third-order stipes are up to 300 mm long. Detailed morphology of thecae unknown, but they appear to be similar to those of *Sigmagraptus praecursor*. Thecal spacing unknown.

Discussion. The main features of the species have already been discussed. Harris & Thomas's (1941) figures give no details of sicular or thecal morphology other than that thecae are slender and of *Sigmagraptus praecursor* type. The species is found in the Chewtonian and Castlemainian (Ca 1) in Australasia and in the Chewtonian and late Bendigonian of Spitsbergen. Ruedemann's (1902) species *Bryograptus lapworthi*, from Beds 1 and 2 of the Deep Kill section of New York (i.e. in strata equivalent to Bendigonian and Chewtonian age), has a similar irregular rhabdosome form and may well prove to be a senior synonym of *L. irregularis*.

Genus *ACROGRAPTUS* Tzaj, 1969

Type species. *Didymograptus affinis* Nicholson 1869.

Emended diagnosis. Sigmagraptines with stipes of two orders; stipes horizontal to deeply declined, narrow at the proximal end, 0·5 mm wide or less.

Discussion. As originally proposed, *Acrograptus* was an upgrading of Elles & Wood's (1901) informal division of *Didymograptus* species with a declined rhabdosome habit. We do not regard the habit as particularly important; this is shown by the very close resemblance between such species as *Didymograptus filiformis* Tullberg 1880 with declined habit, and *D. gracilis* Törnquist 1890, a normal extensiform, which it would be absurd to place in different genera on the basis of stipe habit alone. However, the structure of the proximal end of the type species of *Acrograptus* shows (Fig. 66a) the long slender sicula, and the proximal siting of th1^1 and th1^2 at different levels on the sicula which we describe here as typical of *Sigmagraptus* and allied forms. There is a group of didymograptid species which show the same structure (e.g. Bouček 1973: pl. 11, figs 2, 5; Mu *et al.* 1979: pl. 27, fig. 13), and it is this character which in our opinion distinguishes *Acrograptus* from other Arenig didymograptids, regardless of overall rhabdosome form. Since the proximal end structure resembles that of *Sigmagraptus,* but differs from that of *Didymograptus (Expansograptus)* or *Didymograptus (Didymograptellus),* it is concluded that *Acrograptus* is more closely related to the *Sigmagraptus–Goniograptus* group than to other species with didymograptid habit. Hence it should be included as a separate genus within the Sigmagraptinae rather than as another subgeneric division of *Didymograptus.*

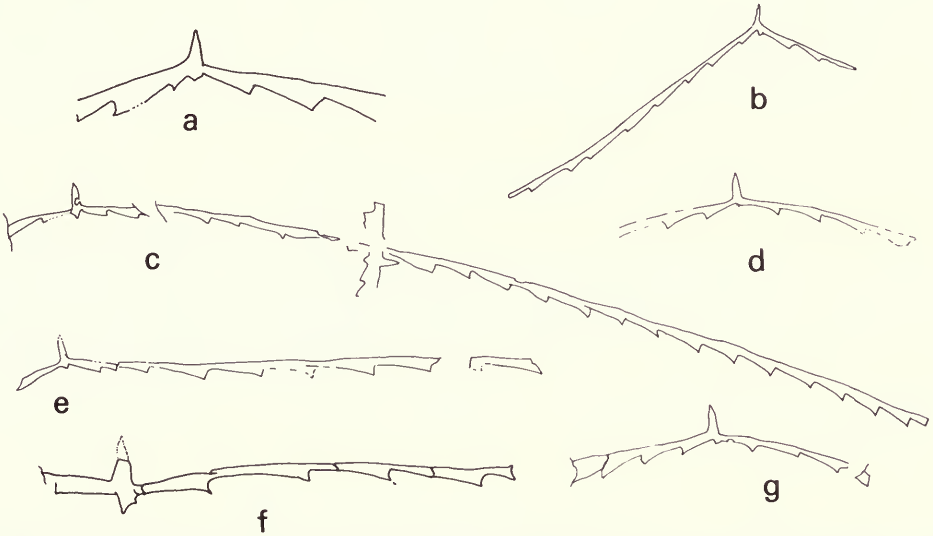


Fig. 66a *Acrograptus affinis* (Nicholson). Holotype, BM(NH) Q3108, proximal end; the original of Nicholson (1869: pl. 11, fig. 20). Skiddaw Slates, × 10.

Fig. 66b *A.* cf. *affinis.* PMO NF654, 60 m above base of Olenidsletta Member on Profilstranda; × 4.

Fig. 66c–g *Acrograptus gracilis* (Törnquist). c, NF824, large specimen from 35 m above base of Olenidsletta Member on Profilstranda; × 4. d, e, NF3329 and NF3328 respectively, 49 m above base of Olenidsletta Member, southern section; × 5. f, Lund University LO923-6t, specimen from the type slab of Törnquist (1890); × 10. g, NF3329, proximal portion, same horizon as c; × 5.

As far as development type is concerned, the well-preserved species *A. lipoldi* described by Bouček (1973) clearly shows isograptid development, which we would expect by comparison with *Sigmagraptus.* The asymmetry of the proximal end may be partly the result of the broader crossing canal connected with the isograptid development type. Bouček interprets another *Acrograptus (A. nicholsoni)* as probably having *artus* development. As we have shown elsewhere, this can be very difficult to interpret from flattened material. However, Bulman (1936*a*: 27) also suggested *artus* development for a Llanvirn species similar in most respects to typical Arenig *Acrograptus,* although he comments that the isolated material is not well-preserved. Skevington (1965) indicated a similar development for a species identical to that of Bulman, although again preservation was imperfect. The initiation of th1^1 is also lower on the sicula than in typical Arenig species. If *artus* development is confirmed for the younger material it seems that there are two possibilities: either these younger species were derived from *Didymograptus (Didymograptus)* with the same kind of development, or (and we consider this more likely) the same kind of reduction of th1^2 occurred in the sigmagraptine lineage that we have proposed in the pendent didymograptid group.

Acrograptus gracilis (Törnquist 1890)

Fig. 66c–g

1890 *Didymograptus gracilis* Törnquist: 17; pl. 1, figs 9–12.

Stratigraphic range. Olenidsletta Member, 35 m to 55 m from base, V_1b–c, Arenig, *Didymograptus protobifidus* Zone.

Material. PMO NF824, NF3328–9, NF3342.

Description. Sicula 1·0–1·1 mm long, and very slender. Theca 1^1 and th1^2 grow out normal to axis of sicula, and at different levels, th1^1 being the higher of the two. Small growth stages are rather common along with *Isograptus scandens* sp. nov. in the dark silt at 55 m above the base of the Olenidsletta Member on Olenidsletta, where they present a distinctive, lop-sided appearance because of the growth of the first two thecae, as shown by Törnquist (1980: pl. 1, fig. 12). The initial growth of the stipes is horizontal, or very nearly so, but distally they may be gently declined, and it is not unusual to find portions of stipes probably belonging to this species preserved twisted in such a way as to suggest that they were originally quite flexible. Our best specimen has one stipe 3 cm long. Lengths of free ventral walls of th1^1 and th1^2 are 1 mm, and all the thecae along the stipe are similarly long and narrow (free ventral walls up to 1·3 mm) and inclined at an extremely low angle. Stipe width at th1^1 is 0·2–0·3 mm and there is a very gradual increase in width of stipes to a maximum of 0·5 mm distally. When a true thecal profile is preserved it is clear that the thecae were flared at the aperture, to generate a slightly acute angle between ventral wall and apertural margin. Distal thecal spacing is 7 in 10 mm.

Discussion. The important character of this species, as Törnquist originally specified, is the horizontal direction of the first two thecae. Our specimens compare closely with the types, which we have examined; although the Spitsbergen examples attain a slightly greater stipe width they are also longer than Törnquist's types. *Didymograptus ellesae* Ruedemann (1904) seems to have a similar habit to that of our largest specimen, with distal declination of the slender stipes. The thecal spacing of this species is stated to be 10–12 in 10 mm, and it is outside the range of *A. gracilis* in this regard.

Acrograptus cf. *affinis* (Nicolson 1869)

Fig. 66b

cf. 1869 *Didymograptus affinis* Nicholson: 240; pl. 11, fig. 20.

Stratigraphic range. Olenidsletta Member, 60 m from base.

Material. PMO NF654.

Discussion. A single specimen from above the range of *A. gracilis* has distinctly declined initial thecae (enclosing an angle of about 120°) and cannot therefore be included in that species. Like *A. gracilis* the thecae are long and narrow, and the stipes are only about 0·4 mm wide distally. Examination of the specimens of *A. affinis* figured by Elles & Wood (1901; including the type) shows similar proportions at a comparable stage of growth, although the specimen figured on their pl. 2, fig. 1a has closely spaced theca, 12 in 10 mm. Bouček's (1973) revision of *A. nicholsoni* shows that this species can include individuals close to *A. affinis,* although distal stipe width is apparently greater in *A. nicholsoni.* Comparative work on populations from the type localities of *A. affinis* and *A. nicholsoni* is needed to clarify the acceptable range of variation of these species. We compare our specimen with *A. affinis* because of its slender stipes.

Family **PHYLLOGRAPTIDAE** Lapworth 1873, emend.

Diagnosis. Development platycalycal, of isograptid type and dextral mode. Virgellar spine present, theca 1^1 originates and develops on antivirgellar (dorsal) side of sicula. Rhabdosome bilaterally symmetrical, composed of two or four stipes, horizontal to scandent.

Discussion. Lapworth's (1873) family Phyllograptidae is here revived to include forms with a virgellar spine on the sicula. All such forms differ fundamentally from the bulk of dichograptoids in their earliest development – th1^1 originates and develops on the antivirgellar (dorsal) side of the rhabdosome rather than on the virgellar (ventral) side. Subsequent development follows the 'orthodox' dichograptoid pattern and is of isograptid, platycalycal, type and dextral mode.

The family, as known at present, comprises two genera, *Phyllograptus* Hall *sensu stricto,* and *Xiphograptus* gen. nov. based on *Didymograptus formosus* Bulman. In both genera, the sicula is relatively short, about 1·5 mm or less in length, and similar in morphology. The two genera, however, differ markedly in morphology of the rhabdosome and their close relationship is apparent only when details of the sicula and earliest development are taken into account. Fortunately, although these features can be clearly seen only in isolated material, the presence of a virgellar spine can usually be determined in flattened material providing preservation is reasonably good as, for example, in *Didymograptus formosus svalbardensis,* discussed below. As details of sicular morphology and earliest development of dichograptoids become more widely known, we think it likely further species will be found to possess virgellar spines and the range of rhabdosome types within the Phyllograptidae will expand.

Genus ***PHYLLOGRAPTUS*** Hall, 1858

Type species. *Phyllograptus typus* Hall 1858.

Revised diagnosis. Quadriserial, scandent rhabdosome with four stipes united along their dorsal margins; median septa separating adjacent thecal series reduced to a framework of fornices and a central columella with an open foramen between thecae of adjacent series. Initial thecae distally reclined.

Discussion. The new information on development and structure revealed by the Spitsbergen material shows that *P. typus* is radically different from phyllograptids of the *angustifolius* group and should be placed in a separate genus. Since it is the type species of the genus *Phyllograptus* Hall, by original designation, phyllograptoids with development and structure of *angustifolius* type (fully described by Holm 1895, Bulman 1936*a* and Skevington 1965) must be transferred to a new genus, for which the name *Pseudophyllograptus* is proposed (p. 241). It is unfortunate that the concept of the genus *Phyllograptus* has, until now, been based largely on the isolated material of *angustifolius* mentioned above.

Since distinction between the two genera is based primarily on features seen only in relief material, a particular problem is posed in trying to assess the affinity of previously described 'phyllograptoids', almost all of which are based on flattened material. The presence of a columella and fornical foramina can sometimes be inferred in flattened specimens (e.g. Mu *et al.* 1979: pl. 42, fig. 6; pl. 43, figs 18, 19) as can the reclined growth of proximal thecae and the initially low angle of inclination of subsequent thecae. The somewhat pointed proximal rhabdosome outline and sicular (virgellar) spine of *Phyllograptus, sensu stricto,* can usually be determined. The sicular spine, which is prominent in the Spitsbergen growth stages, has to be looked for carefully in mature rhabdosomes. It is, of course, a greatly enlarged feature in Hall's type material from Levis and its importance lies not in its size but in its presence.

Species. *Phyllograptus typus* Hall 1858, *P. anna* Hall 1865, *P. ilicifolius* Hall 1858, *P. uniformis* Ge (*in* Mu *et al.* 1979) and *P. acuminatus* Chen & Xia (*in* Mu *et al.* 1979).

Re-examination of Hall's type material of both *Phyllograptus anna* and *P. ilicifolius* (discussed below) shows that both can be referred to *Phyllograptus, sensu stricto.*

From their illustrations, several of the forms described by Mu *et al.* (1979) are likely to represent true *Phyllograptus*. Their figures of *'P.' densus* (pl. 42, fig. 26, here synonymized with *typus*) and of *P. uniformis* (pl. 43, figs 17–19) both show what appears to be the central columella and a double row of fornical foramina and both have the characteristically pointed proximal end, as has their *P. acuminatus* (pl. 40, figs 10–13).

The correct generic reference for many described phyllograptoids, however, must remain in doubt until further details of their structure and development are known.

Phyllograptus typus J. Hall 1858

Figs 67a–f, 70a–h, 71a–l, 72–74; Pl. 4, figs 4, 10

1858 *Phyllograptus typus* J. Hall: 137.
1865 *Phyllograptus typus* Hall; J. Hall: 119; pl. 15, figs 1–12.
1947 *Phyllograptus ilicifolius* var. *major* Ruedemann: 318–319; pl. 53, fig. 21.
1960 *Phyllograptus typus* Hall; Berry: 58; pl. 10, figs 13, ?1, ?11.
1963 *Phyllograptus ilicifolius* var. *major* Ruedemann; Ross & Berry: 83; pl. 3, fig. 17.
1976 *Phyllograptus densus* Törnquist; Legg: 27–28; pl. 8, fig. 39.
1976 *Phyllograptus loringi* White; Braithwaite: 38–40; pl. 7, figs 29–31.
1977 *Phyllograptus ilicifolius major* Ruedemann; Carter & Churkin: 14–15; pl. 1, fig. 4.
1979 *Phyllograptus densus* Törnquist; Mu, Ge, Zhen, Ni & Lin: 123–124; pl. 42, figs 26, ?25.

Type material

LECTOTYPE. The specimen GSC 942c, figured by Hall (1865) as pl. 15, fig. 7, carries the label 'Type'. So far as we are aware, neither this specimen, nor any other, has been formally designated as type specimen. For the reasons discussed below (see 'Discussion') this specimen is not thought to be suitable for lectotype.

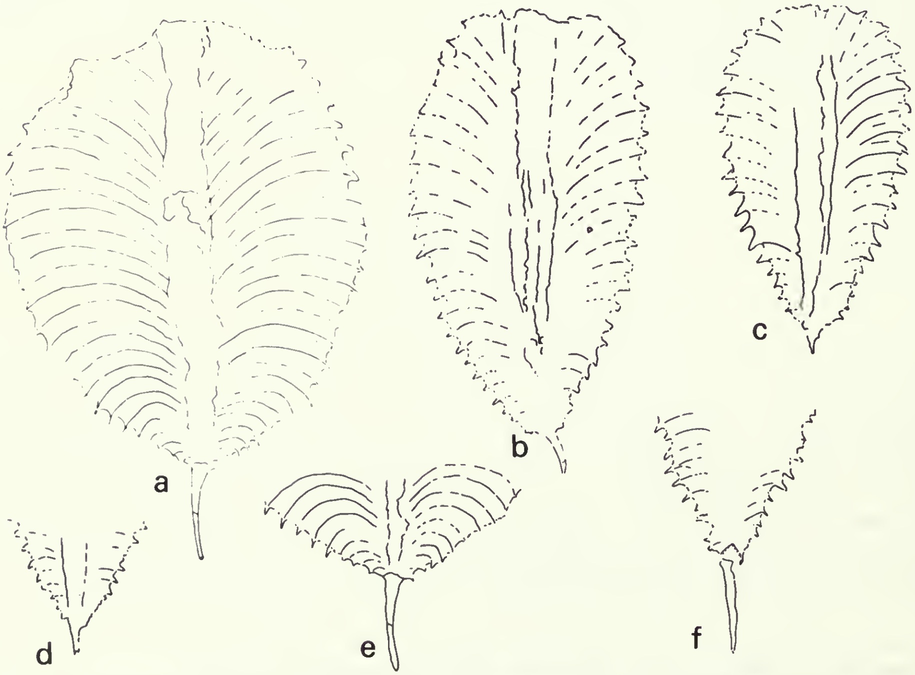


Fig. 67 *Phyllograptus typus* (Hall), type series. a, e, **lectotype,** GSC 942b, whole rhabdosome (× 2) and proximal part (× 3) respectively. Specimen figured by Hall (1865: pl. 15, fig. 1). b, specimen on same slab (GSC 942) as the original of Hall (1865: pl. 15, fig. 10), poorly preserved, and with small spine; × 3. c, specimen on back of slab with original of Hall (1865: pl. 15, fig. 2); poorly preserved but outline and interthecal lines can be seen; × 3. This specimen and that of b, with their pointed proximal regions and relatively inconspicuous spines, most closely match the Spitsbergen forms. d, proximal part of specimen in same slab as that of b; × 3. f, proximal part of specimen preserved in same slab as b, showing pointed proximal region; × 3.

Specimen GSC 942b (of the Geological Survey of Canada, Ottawa), figured by Hall (1865) as pl. 15, fig. 1 and refigured here (Fig. 67a) is here designated **lectotype**. It is about the best preserved of the specimens in the type series, none of which clearly shows details of the proximal end or of internal rhabdosome structure.

Paralectotypes. Other specimens held by the Geological Survey of Canada and examined by us are GSC 942a, c–g, figured by Hall (1865) as pl. 15, figs 1, 2, 4, 5, 7, 10 and 12. In addition at least 10 other, unfigured specimens are present in the same slabs providing a relatively large population of type material. None are well preserved and many have lost much of the original carbonized periderm; it is possible that they have deteriorated considerably since Hall examined them. As far as can be determined, Hall's figures give a reasonably accurate portrayal of the specimens.

Stratigraphic horizon. Raymond (1914) lists *P. typus* from Zone B together with *Tetragraptus fruticosus* and Bulman (unpublished MS) adds *Didymograptus nitidus* and *P. ilicifolius*. The horizon is thus Bendigonian, or lower Arenig.

Description of type material. The sicula and details of the proximal region are not visible in any specimens, nor is internal rhabdosome structure. Rhabdosome outline varies widely from almost circular to elongate and the ratio of maximum width to length ranges from 0·29 to 0·85 with modal value of about 0·5 (Fig. 68). Most rhabdosomes have a prominent spine extending

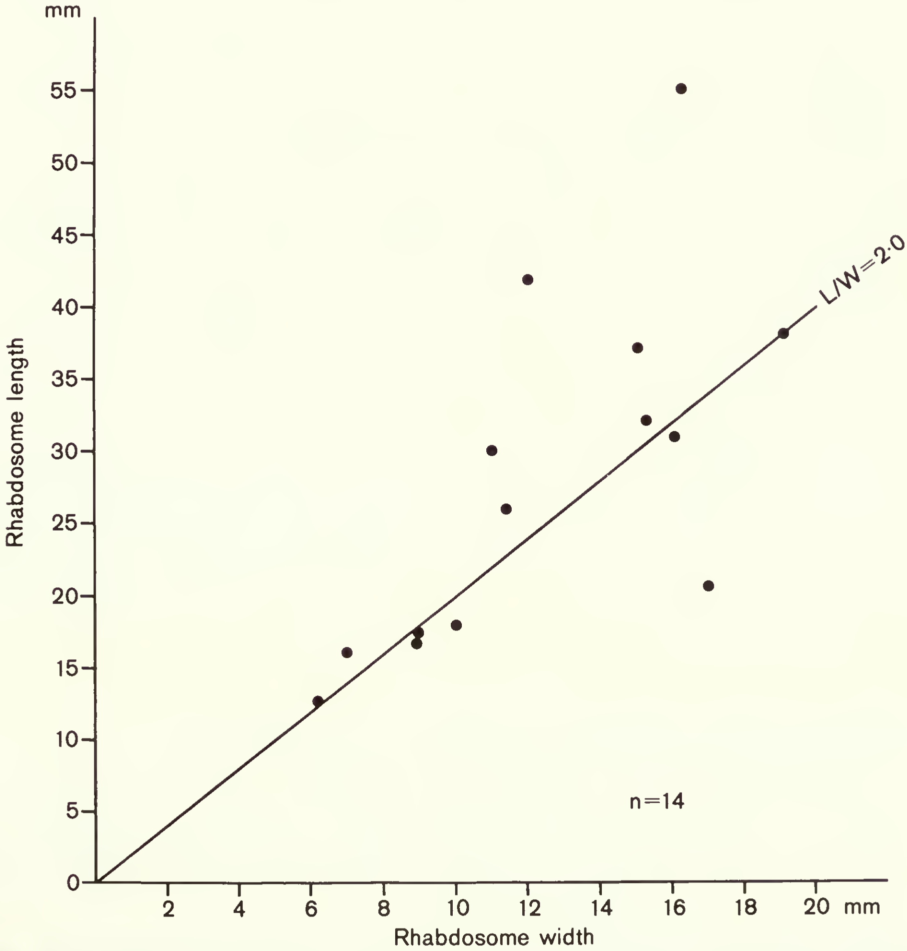


Fig. 68 *Phyllograptus typus* Hall, type population; rhabdosome width plotted against rhabdosome length.

from the proximal margin. Presumably this represents an enlarged virgellar spine. In the larger rhabdosomes the spine has a very broad base, and in a few it obscures the apertures of proximal thecae. In the specimens examined by us the length of the longest spine (that of Hall's pl. 15, fig. 7) is 6·5 mm, but the specimen of Hall's pl. 15, fig. 8 is shown by him to have a spine 10 mm long.

Thecae have relatively low initial inclination and are curved, strongly in the proximal region but progressively less strongly towards the distal end. Apertural outlines are not clearly shown in any specimen. Thecae are most densely spaced in the proximal region and most widely spaced in the distal parts of large rhabdosomes; the difference in thecal spacing between the two parts of the rhabdosome ranges from 1 to about 3 or 4 thecae in 10 mm. In large rhabdosomes measurements were taken in the mid-region of the rhabdosome for comparison with smaller forms. Spacing ranges from 10 to 13 in 10 mm, with a modal value of 10 (Fig. 69). The strong positive skew in the distribution may reflect the small sample size but may, in part, result from a weighting of the high (close spacing) end owing to inclusion of some small specimens.

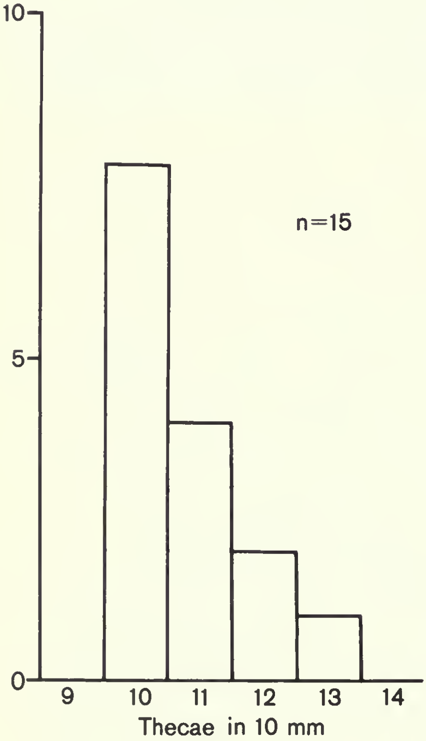


Fig. 69 *Phyllograptus typus* Hall, type population, frequency distribution of thecal spacing. The strong positive skew may simply reflect the small sample size but may, in part, result from attenuation of the high (close spacing) end of the range owing to the inclusion of some small specimens.

Range in rhabdosome form, spine development, thecal inclination and curvature is best appreciated by examining Hall's figures together with those figured here.

Discussion. From Hall's figures it might be supposed that two populations are represented; those of his pl. 15, fig. 10 have relatively small rhabdosomes with less conspicuous sicular spines and more wedged-shaped proximal outlines whereas those of the remaining figures have large, rapidly expanding and sometimes irregularly shaped rhabdosomes and enormous sicular spines. None of the specimens of his fig. 10 are well preserved and the lectotype has been chosen from among the large specimens. The smaller wedge-shaped specimens are here regarded as conspecific with the Spitsbergen material assigned to *P. typus* and the question of their identity with the larger forms is crucial in view of the implications for the species of the unusual (and diagnostic) development and internal structure revealed in the Spitsbergen material. Fortunately, among the unfigured specimens in Hall's collection is a group (particularly those on the slab, 942d, with the specimen of pl. 15, fig. 2) which bridges the gap and indicates that all of Hall's material most probably represents a single population, with wide variability in rhabdosome size and outline and in development of the sicular spine. There are no other taxa present and the lithology of all slabs is the same, a dark carbonate-rich siltstone.

The large forms may simply be 'overgrown' or 'gerontic' rhabdosomes. Continued growth of proximal thecae would increase the rate of rhabdosome expansion and result in a more rounded proximal end. Proximal thecal curvature would increase and their distal portions would become more markedly pendent. These features are well shown by the lectotype. The slightly irregular outlines of several rhabdosomes suggest variation in growth rate and the massive sicular spine indicates overgrowth, presumably by additional layers of cortical tissue. The process seems to be most developed in the specimen (GSC 942c) of Hall's pl. 15, fig. 7 and for this reason the specimen is deemed unsuitable for lectotype.

Phyllograptus ilicifolius major Ruedemann (1947) is clearly a synonym of *P. typus*. The holotype (Ruedemann 1947: pl. 53, fig. 21, refigured by Ross & Berry 1963: pl. 3, fig. 17) from Nevada has a proximal spine, proximally pointed rhabdosome and similar thecal spacing. Its distinction from *P. typus* was discussed neither by Ruedemann nor Ross & Berry. The specimen figured by Carter & Churkin (1977: pl. 1, fig. 4) as *P. ilicifolius major* has a larger rhabdosome and more prominent proximal spine, like that of the Levis forms, but slightly more closely spaced thecae (12–14 in 10 mm). The horizon for the species in western U.S.A. is given as *D. protobifidus* Zone. The specimen figured by Legg (1976: pl. 8, fig. 39) from Fauna 3b (Bendigonian–Chewtonian), as *P. densus* Törnquist, bears a proximal spine and pointed proximal end; its higher thecal count (13–14 in 10 mm) may reflect its relatively small size and be equivalent to the more densely spaced proximal thecae of large specimens. Specimens figured as *P. densus* from Zone N3b of *Didymograptus deflexus* (about Chewtonian) of south-west China by Mu *et al.* (1979: 123–124; pl. 42, figs 24?, 25?, 26) show an axial structure with what appears to be a central columella separating a double row of fornical foramina. Overall rhabdosome shape, thecal inclination and curvature lie within the range of *P. typus*, with which it is included here. Braithwaite's description and figures (1976: 38–40; pl. 7, figs 29–31) of supposed *P. loringi* White, from his Zone 5 of Utah, match well with *P. typus*.

The wide range in rhabdosome size and proportions was discussed and illustrated by Hall, and also commented upon by Ruedemann (1947) and Berry (1960). These characters thus appear to be of limited use in diagnosis. However, the narrow, elongated rhabdosome form of *Pseudophyllograptus angustifolius* is rarely achieved in the various North American and Spitsbergen populations in which a broad oval outline is most common. Similarly, thecal spacing, although strongly modal at 10 thecae in 10 mm, ranges widely and is unlikely to justify the faith placed in it as a diagnostic character by some authors. Because of the denser thecal spacing in immature rhabdosomes it is likely that they have often been confused with *Phyllograptus anna* Hall (see p. 286).

Spitsbergen material

STRATIGRAPHIC HORIZON. Specimens with the diagnostic axial structure are known from 40–43 m, 75 m and 88–90 m levels in units V_1–V_2 of the Valhallfonna Formation. Specimens showing the proximal spine are present at the 25 m and 75 m levels. All phyllograptoids of this interval (25 m–90 m) appear to comprise a single variable group and are included in the species. In addition, specimens from the 12–15 m and 93 m levels have a pointed proximal margin, a similar range in rhabdosome shape, and are also included. Total range is thus 12 m–93 m level, V_1–V_2, and embracing all the middle Arenig.

MATERIAL. F3716, F3801, F4005, F4055, F4084, F4098, F4169, F4270, F4271, ?F4218. PMO NF625, NF636, NF751, NF760, NF765, NF2046, NF2049, NF2050, NF2065, NF2815, NF3173, NF3390–1. SM A105794, A105810, A109732, A109737.

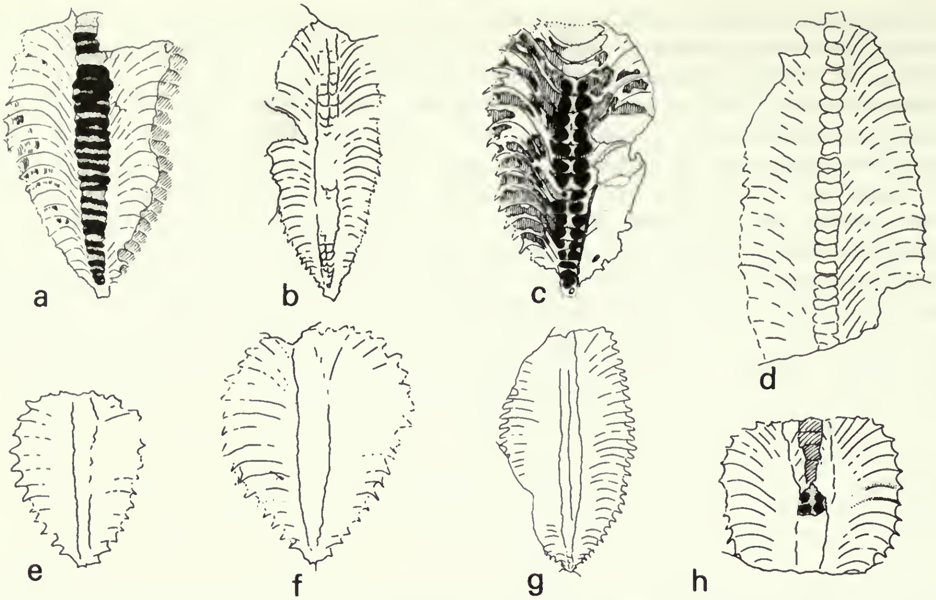
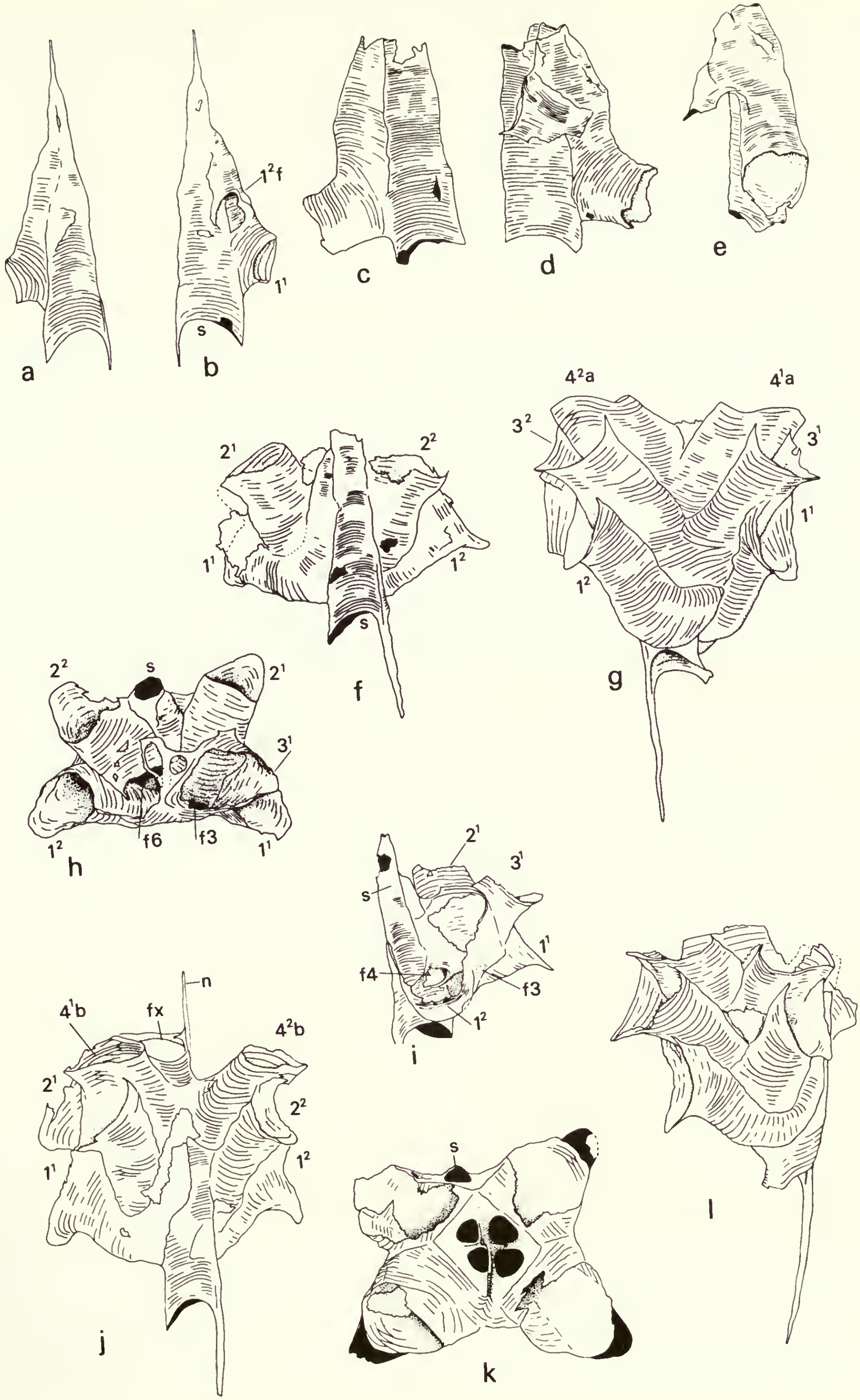


Fig. 70 *Phyllograptus typus* Hall, Spitsbergen population. a, PMO NF760, specimen in relief in limestone showing transverse cross sections of upper thecal series, broken off near the axial region and exposing short lengths of interthecal septa (stippled). 74·5 m above base of Olenidsletta Member, type section; × 4. b, NF3362, rather poorly preserved specimen from 40–43 m above base of Olenidsletta Member; × 2. c, NF3173, specimen in relief and partially etched revealing double row of internal fornical foramina and central columella. Same horizon as a; × 4. d, SM A109737, proximal end broken off. 93 m above base of Olenidsletta Member, type section; × 2. e–g, PMO NF3176, NF2049 and NF2065 respectively. Virgella clearly showing in f. All from 23–25 m above base of Olenidsletta Member, southern section; e and f × 2; g × 3. h, SM A109732, upper stipe broken off to reveal, near mid length, the fornical foramina; × 3. This form resembles *P. rotundatus* Monsen: see Pl. 4, fig. 7.

Description of isolated material. Sicula bears a short nema up to 0·5 mm long. Details of the prosicula are unknown. The metasicula bears a prominent virgella which projects beyond the apertural margin by up to 0·8 mm. It appears to be most robust in the more advanced growth stages, suggesting that it was built up with cortical tissue after completion of growth of the

Fig. 71 *Phyllograptus typus* Hall, isolated growth stages. a, b, PMO NF751, early growth stage with theca 1^1 partly formed and the foramen (1^2f) to th1^2 formed, obverse and reverse views. Note weakly developed virgella and antivirgellar side origin of th1^1. c, d, e, NF3390, incomplete growth stage obverse, reverse and lateral (stipe^1 side) views respectively. Theca 1^1 has diverged from the sicula and the arch through which th2^1 would grow can be seen. f, h, NF3391, growth stage with apex of sicula broken off; first 4 thecae (1^1, 1^2, 2^1, 2^2) have formed. Obverse view (f) shows sicula has not yet become enveloped by proximal thecae, and prominent virgellar spine. Top view (h) shows the commencement of formation of columella, and first interthecal foramen (from th3^1 to th4^1a) and the foramina, f3 ($2^1/3^1$) and f6 ($2^2/4^2$a). s = sicula. i, NF622, specimen dissected to reveal foramen (f4) between th1^2 and th2^2. Position of foramen (f3) between th2^1 and th3^1 indicated. Thecae 2^2, 3^2 and part of 1^2 have been removed. j, NF3312, advanced growth stage with three thecae on each stipe showing reclined attitude of distal portions of proximal thecae. Note that apical part of sicula has become enveloped by thecae 4^1b and 4^2b. Fornix (fx) lies behind, and is *not* attached to, nema (n). g, k, l, NF3314, viewed from interangle between stipes ^{1}a and ^{2}a (g), ^{1}a and ^{1}b (l) and top (k). Top view shows four quadrant-shaped interthecal foramina in square plate-like structure formed of the four adjacent interthecal septa in the axial region. Note that thecae of adjacent thecal series remain in lateral contact for some distance beyond the central axial region. All specimens from 74·7 m above base of Olenidsletta Member, type section. All × 30.


a
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sicula and the first few thecae. The downward deflection of fuselli into the virgella can be traced back to the mid-region of the metasicula, suggesting that the virgella begins to form, and the ventral side of the sicula is defined, at an early stage. The dorsal margin of the sicula is extended into a prominent lip which projects well beyond the level of the base of the virgella. This feature, also, develops at an early stage of growth of the metasicula.

Length of the sicula, to the tip of the dorsal margin, is 1·2–1·4 mm, and dorsoventral width at the aperture ranges from 0·3 to 0·35 mm. Variability in the length of that portion of the metasicula which projects below the ventral walls of the first two thecae is shown in Fig. 71f, j.

The sicula remains free on the obverse side of the rhabdosome up to the level of th2^1, after which its apical portion becomes incorporated within the rhabdosome wall (Fig. 71j). The nema becomes embedded along the junction of the two thecal series, ^{1}b and ^{2}b. The nema is not continuous with the axial column but is linked with it by fornices ('flying buttress' structures) described below.

The distal portions of all proximal thecae are directed upwards at about 45° to the stipe axis, and the proximal rhabdosome margin has a rather pointed outline.

PROXIMAL DEVELOPMENT. This has been determined from two early growth stages (Fig. 71a–e) and several advanced growth stages, the outer rhabdosome walls of some of which have broken away exposing internal structure.

Details of the prosicula are unknown. Origin of th1^1 is not clear but it appears to arise from either the prosicula or from near the top of the metasicula, on the dorsal side.

In its early development it forms a 'hood' which soon expands out into an arch allowing room for the developing th2^1 (Fig. 71e). Theca 1^1 grows well down the sicula before curving sharply away and looping around the base of th2^1, its distal portion growing strongly upwards and outwards and forming the basal theca of stipe ^{1}a. The dicalycal theca, 1^2, originates *via* a broad foramen from th1^1 (Fig. 71b), grows down and across the sicula in a dextral sense and curves

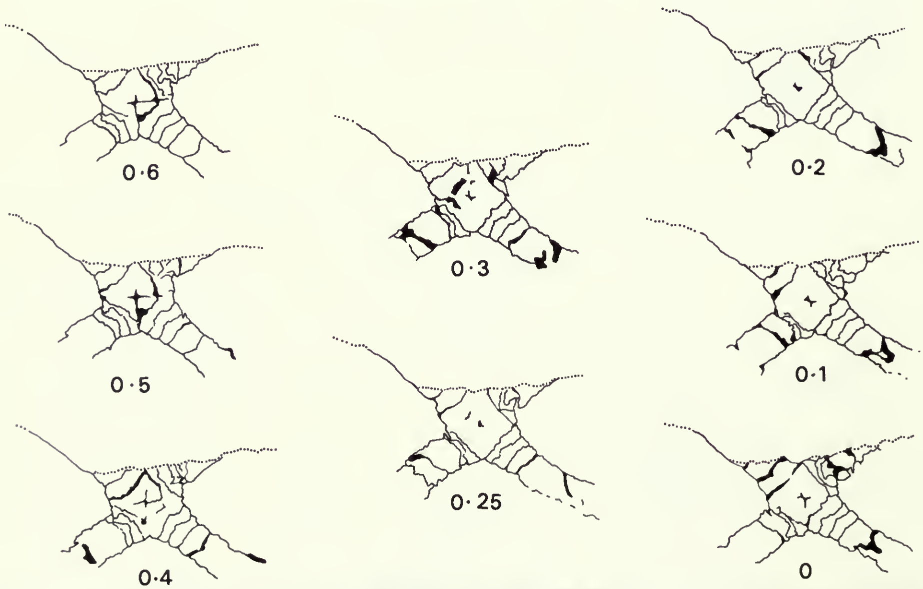

Fig. 72 *Phyllograptus typus* Hall, serially ground sections, PMO NF765, × 4. Specimen has partially collapsed but is sufficiently intact to reveal some details of internal structure. Section level shown by number in mm above basal section. Sections 0–0·25 show cruciform columella in centre of axial region with wide openings (fornical foramina) between thecae of laterally adjacent series. Sections 0·4–0·6 pass through the region of the fornices, section 0·6 intersecting two fornices. Because of the slight spiral offsetting of fornices (and possibly damage suffered by the specimen) no single section passes through all four fornices.

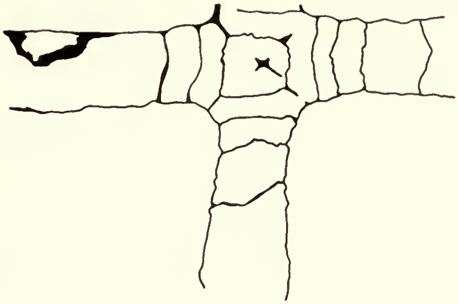

Fig. 73 *Phyllograptus typus* Hall. PMO NF760, transverse section through mature part of rhabdosome to show internal structure. Top stipe lies off edge of slab. Cruciform columella in centre with wide openings (fornical foramina) between thecae of laterally adjacent thecal series, except for where fornix has been intersected (lower right); × 8.

sharply away from it at about the same level as does th1^1. It then loops around the base of the developing th2^2 and grows upwards and outwards forming the basal theca of stipe ^{2}a and matching, in its distal region, the attitude of the distal part of th1^1. The first two thecae are thus considerably longer than subsequent proximal thecae. Theca 2^1 arises shortly after the origin of th1^2 and grows across the line of th1^1, in its upward growth forming the basal theca of stipe ^{1}b. It gives rise to the dicalycal theca, 3^1, through a small round (? resorption) foramen (f3, Fig. 71h, i). Theca 4^1b is given off through a wide foramen as is the 'sibling' theca 4^1a. At this stage of development, stipe ^{1}a is comprised of three thecae, 1^1, 3^1 and 4^1a and stipe ^{1}b is comprised of two thecae, 2^1 and 4^1b.

On the th1^2 side, th2^2 arises through a small round foramen (f4) like that of th3^1 and forms the basal theca of stipe ^{2}b. It gives off, through a wide open foramen (f6, Fig. 71h), the dicalycal th3^2 which in turn gives off, firstly th4^2b then th4^2a. At this point, stipe ^{2}a is composed of the three thecae, 1^2, 3^2 and 4^2b and stipe ^{2}b is composed of the two thecae, 2^2 and 4^2b. The four stipes are developed, from this point on, by unicalycal budding.

INTERNAL RHABDOSOME STRUCTURE. Internal structure of the mature rhabdosome has been determined from a partially etched specimen (Fig. 70c) in which one thecal series has broken away exposing the axial region, from serially ground sections (Figs 72, 73) of the mature part of the rhabdosome, and from advanced growth stages (Fig. 71i–l).

The four stipes are united along their dorsal margins, not by a set of four median septa as in *Pseudophyllograptus angustifolius* (clearly illustrated by Holm 1895: pl. 14, fig. 12) but by a complex internal network of struts and horizontal perforated plates. The interthecal septum between thecae in any thecal series (i.e. in any one 'stipe') becomes sharply horizontal as the axial region is approached and is perforated by a comparatively small quadrant-shaped aperture, the interthecal foramen (Fig. 71k). The septum is united with its neighbours of the

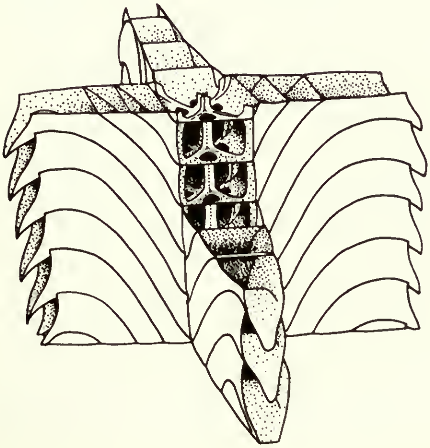

Fig. 74 *Phyllograptus typus* Hall. Cut-away diagram showing internal rhabdosome structure.

adjacent thecal series in the axial region to form an axial platform. Each segment of the platform is slightly offset from the level of the adjacent segment and the platform is spirally curved. Thus in the section series (Fig. 72) the four interthecal foramina are not intersected by any one section. The lateral thecal wall within the axial region is largely reduced to an arched strut, like a flying buttress, here termed the *fornix,* one at the level of each interthecal septum. A wide opening, the *fornical foramen* is thus left between thecae of adjacent thecal series.

The innermost margins of the lateral thecal walls are united to form a thickened column, the *columella,* at the centre of symmetry of the rhabdosome, clearly seen in serial sections (Fig. 72). Fig. 71k shows that the columella develops independently of the sicula and nema.

Growth stages indicated that the fornices are primary structures formed during the building of the rhabdosome and the fornical foramina are not secondary resorption features, like the accessory foramina in *Pseudotrigonograptus minor* (Fortey 1971).

COMMENTS ON PROXIMAL DEVELOPMENT AND STRUCTURE. Origin and subsequent growth of theca 1^1 on the antivirgellar side of the sicula is a departure from the usual dichograptoid pattern. The thecal budding plan is shown in Fig. 75. Initial development conforms with the isograptid type and is dextral.

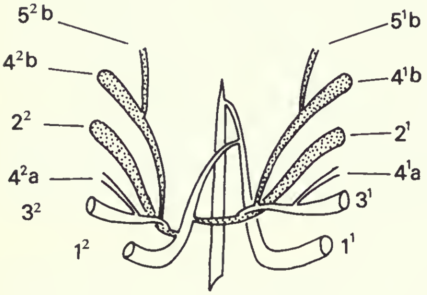

Fig. 75 *Phyllograptus typus* Hall. Thecal diagram for proximal development.

The second-order dichotomy on the stipe^1 side is based on dicalycal th3^1 and is sinistral, whereas that on the stipe^2 side is based in th3^2 and is dextral. All three dicalycal thecae thus grow out on the reverse side of the rhabdosome. The interthecal foramina which open into thecae 1^2, 3^2, 4^1a, 4^1b, 4^2a and 4^2b are large, open, primary apertures, but those opening into thecae 2^2 and 3^1 are small and round and are possibly resorption foramina. That opening into th2^1 has not been clearly seen but appears to be large and primary.

A striking feature of the proximal region is the reclined attitude achieved by the proximal thecae, particularly thecae 1^1 and 1^2, shown clearly by the isolated growth stages (Figs 71g, j). In this respect, the species (and the genus) is unique among dichograptoids, even among such scandent forms as *Skiagraptus, Cardiograptus* and *Pseudophyllograptus* where proximal thecae grow essentially downwards or outwards rather than upwards. It resembles, rather, the early diplograptids especially streptoblastic glyptograptids of the *austrodentatus* group (Bulman 1963).

Another unusual feature is that the first two thecae 1^1 and 1^2 form the basal thecae of the adjacent pair of second-order stipes, ^{1}a and ^{2}a respectively. This is an unexpected departure from the general graptolite rule of maintaining symmetry in development and an important point of difference from *Pseudophyllograptus* where the initial thecae do not form part of the second-order stipes but lie below, and medially between them, as in *Tetragraptus bigsbyi.*

DESCRIPTION OF NON-ISOLATED MATERIAL. Rhabdosome size and shape are extremely variable and scarcely any two specimens, even from the one bedding plane, are closely similar. Maximum rhabdosome length is 35 mm, maximum width is 14 mm. The ratio of maximum width to length ranges from 0·3 to 0·65 (Fig. 76) and outline shape varies from squat and ovate to elongate. The distal margin of incompletely grown rhabdosomes is bluntly terminated (Fig. 70e, h). The proximal margin tapers to a point and the sicular (virgellar) spine is only rarely

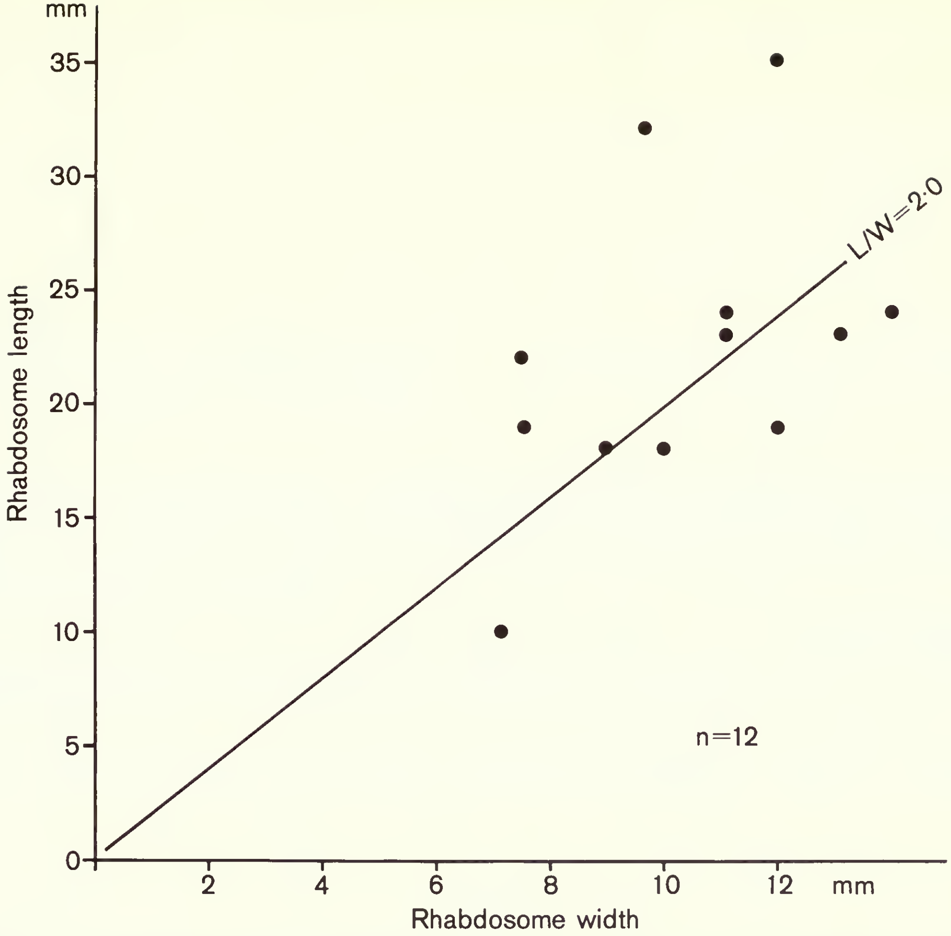

Fig. 76 *Phyllograptus typus* Hall, Spitsbergen population. Rhabdosome maximum width plotted against rhabdosome length, showing wide variation in rhabdosome proportions. Incomplete specimens (not plotted) show that total range of variation is greater than that shown.

visible. The attitude of proximal thecae is seldom determinable in flattened material but specimens from the 25 m level (Fig. 70e, f) appear to have initial thecae that are somewhat less reclined than those from the 75 m level. However, isolated but flattened growth stages from the 15–23 m level (A105810) show strongly reclined early thecae.

In their initial growth, thecae have relatively low inclination (40° or less) but curve sharply and reach an inclination greater than 90° near their apertures. Their lateral width is greatest near the axial region where they have a transversely tabular cross section (Fig. 70a). Except for the proximal few thecae, which have free ventral walls, thecae overlap for almost their entire length. Apertural margins are projected into a prominent ventral lip. The axial region of the rhabdosome increases in width from about 0·5 mm near the proximal end to over 2 mm in the middle part of the rhabdosome (Fig. 70c).

Thecae are spaced 10 to 14 (most commonly 12) in 10 mm in the mature part of the rhabdosome (Fig. 77). Thecal spacing is denser in the proximal region and immature rhabdosomes give thecal counts of 16 or more in 10 mm. There is no progressive change in thecal spacing in successively higher stratigraphical levels (Fig. 78).

FUNCTIONAL INTEPRETATION. The functional purpose of the large fornical foramina and struts, in place of a continuous peridermal wall, between thecal series in the axial region can only be

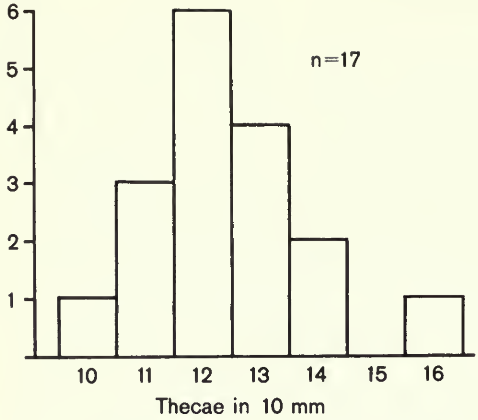

Fig. 77 *Phyllograptus typus* Hall. Frequency distribution of thecal spacing (taken to nearest whole number) in Spitsbergen population, showing wide range of variation.

guessed at. They would have had the effect of lightening the rhabdosome without reducing its rigidity, and thereby aiding in buoyancy. This is unlikely to have been their primary function, however, since it will be seen from the sections that the amount of weight saved is a minimal proportion of the total rhabdosome weight. It seems more likely that they existed to allow communication, either direct or indirect, between zooids of adjacent thecal series, but for what purpose is unclear.

What is clear is that construction of the axial skeletal structures required highly integrated acitivity on the part of the graptozooids, throughout the development of the rhabdosome, and closely concordant budding within each of the four thecal series. The columella appears to be without analogy among the graptoloids unless it is equivalent to the pseudovirgula of monograptids. It is built up along with the rhabdosome and never projects far beyond the distal

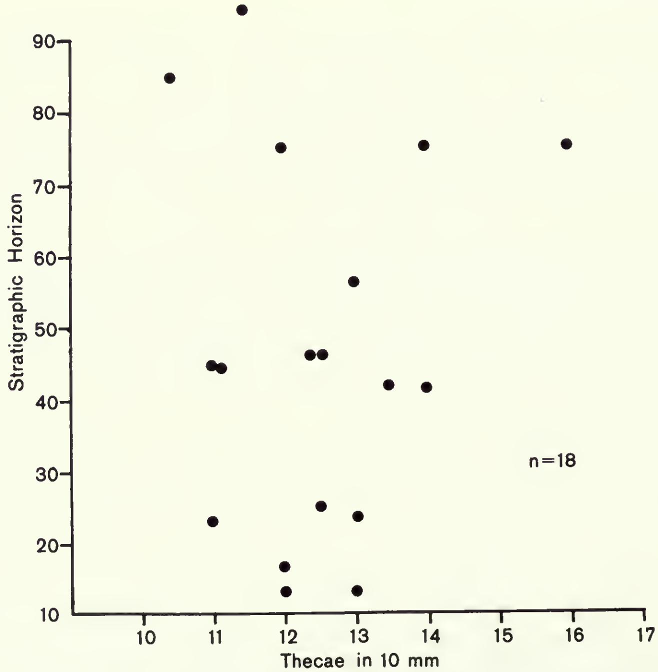

Fig. 78 *Phyllograptus typus* Hall. Thecal spacing (taken to nearest whole number) in Spitsbergen specimens plotted against stratigraphical level (metres above base of Olenidsletta Member). There is no progressive trend through the considerable stratigraphic interval of its occurrence.

rhabdosome margin. It could thus not have acted as an attachment organ and there is no evidence that the rhabdosome was suspended, although the sicula, with its short nema, and earliest growth stages may have been.

DISCUSSION. The species is readily distinguished by its peculiar internal rhabdosome structure and proximal development and structure. Unfortunately neither of these regions is readily examined in flattened specimens. In incompletely flattened specimens where the upper stipe has broken away right back to the axis, the fornical foramina and columella can be seen (Fig. 70c); where the inner margin of the upper stipe still remains, as in Fig. 70a, d, only the matrix-filled thecal interiors are exposed, providing no clue as to internal structure.

The pointed proximal end can usually be determined in flattened specimens, but angle of inclination of proximal thecae is commonly obscure.

The Spitsbergen form most closely matches *Phyllograptus typus* Hall and *P. ilicifolius* Hall. The absence of an overgrown virgellar spine from mature rhabdosomes suggests *P. ilicifolius*, but the persistently pointed proximal rhabdosome outline and wide variability in rhabdosome form and proportions, together with the large size attained by some rhabdosomes and the prominence of the virgellar spine in growth stages, suggest that the Spitsbergen form is best identified with *Phyllograptus typus*. The slightly higher thecal spacing modal value may be a reflection of the generally smaller size of rhabdosome in the Spitsbergen populations, and thus of the closer thecal spacing in the proximal region, but the wide range is similar in both the Spitsbergen and Levis populations.

Internal rhabdosome structure and proximal development and structure are, of course, unknown in the type population of *typus* and these features, revealed by the Spitsbergen material, provide important diagnostic characters for the species and for the genus *Phyllograptus*.

RELATIONSHIPS AND ANCESTRY. Several features of development and structure indicate that the species is unlikely to have been derived from an ancestor of *Tetragraptus bigsbyi* type, as seems probable for *Pseudophyllograptus* (Bulman 1936*a*). The rhabdosome could not have been formed by, in effect, concrescence of the stipes of a reclined tetragraptid. While it could be argued that the internal rhabdosome structure was secondarily derived from a ‘normal’ pseudophyllograptid, the strongly reclined initial thecae and their alignment with the two adjacent stipes ^{1}a and ^{2}a, the presence of a virgellar spine, and the antivirgellar development of th1^1 are all features unknown in any tetragraptid.

It is here thought that sicular morphology and the antivirgellar origin and growth of th1^1 may provide a clue to its relationship with other species. These features would unite it with such species as *Xiphograptus formosus formosus* and *X. formosus svalbardensis*. Ancestry of such a group, however, remains unclear.

Phyllograptus anna Hall 1865
Fig. 79a–d

1865 *Phyllograptus anna* J. Hall: 124; pl. 16, figs 11–16.
1902 *Phyllograptus anna* Hall; Elles & Wood: 101–102, figs 60a–b; pl. 13, figs 6a–f.
1904 *Phyllograptus anna* Hall; Ruedemann: 714–717, text-figs 98–99; pl. 15, figs 23–30.
1979 *Phyllograptus anna* Hall; Cooper: 68, fig. 40; pl. 6g; pl. 10g.

LECTOTYPE. Slab GSC 938a, figured by Hall (1865: pl. 16, fig. 15) and refigured here (Fig. 79a) is here designated as **lectotype**. Preserved in the Geological Survey of Canada Museum, Ottawa.

PARALECTOTYPES. GSC 922f, 938 and 938a; specimens figured by Hall (1865: pl. 16, figs 11, 13, 14, 15, 16) held by the Geological Survey of Canada. The slab 938a has, in addition, more than 60 other rhabdosomes of the species, of which three are figured here (Fig. 79b–d).

STRATIGRAPHIC HORIZON. Raymond (1914) and Bulman (unpubl. MS) list *P. anna* from Zone C3 of the Levis Shales at Levis, Quebec, together with *Didymograptus bifidus*.

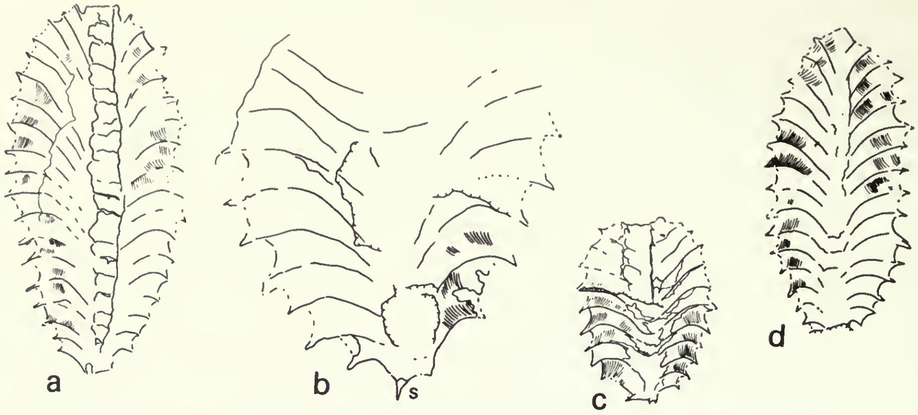

Fig. 79 *Phyllograptus anna* Hall, type series. a, **lectotype** GSC 938a, original of Hall (1865: pl. 16, fig. 15); × 4. b, proximal region of specimen in same slab as lectotype showing incipient spine on sicula (s) and reclined growth of proximal thecae; × 8. c, small specimen in same slab as lectotype clearly showing proximal thecae; × 4. d, specimen in same slab as lectotype; × 4.

Discussion. The species is included in the present discussion in order to clarify its relationship with *Phyllograptus typus* and *Pseudophyllograptus angustifolius*. Traditionally it has been recognized primarily by its small size and closely-spaced thecae. From the refigured lectotype and paratypes, however, it can be seen that several features of rhabdosome morphology are shared with *P. typus*. The low initial angle of thecal inclination and the reclined attitude of the proximal thecae are particularly noticeable. Furthermore, in the specimens of Fig. 79b, c the sicula protrudes from the proximal end of the rhabdosome and bears a short virgellar spine. The general aspect of the proximal region is undoubtedly similar to that of *P. typus* and *P. ilicifolius*, with which species it is here thought to be most closely related. It is therefore included in the genus *Phyllograptus, sensu stricto*.

Thecal spacing is difficult to determine because of the small size of the rhabdosome, but is approximately 6·5 in 5 mm (i.e. 13 in 10 mm) measured in the middle third of the rhabdosome of the two largest figured rhabdosomes. This figure is slightly smaller than that given by Hall (14·5 in 10 mm) and Elles & Wood (14–16 in 10 mm), and considerably smaller than that given by Ruedemann (16–20 in 10 mm). Ruedemann's illustations, however, would suggest that at least some of his specimens have a somewhat wider spacing of about 14–16 in 10 mm when measured as above. Internal rhabdosome structure cannot be clearly determined in any of the type specimens.

The species closely resembles early growth stages from Spitsbergen assigned to *P. typus* and it is possible that it represents a growth stage of *typus* or *ilicifolius*. Unfortunately there are no early growth stages of either *typus* or *ilicifolius* from Levis available for comparison. From the Spitsbergen growth stages it is distinguished by its tapered, rather thin, bluntly terminated distal end, suggesting that it represents a mature rhabdosome rather than a growth stage. On this rather tenuous evidence, and until stratigraphically controlled population studies are carried out on the Levis section, *Phyllograptus anna* is maintained as a distinct species.

The forms described as *P. anna* by Braithwaite (1976: 32–35; pl. 7, figs 9–21) have truncated distal rhabdosome margins, suggesting that they are immature rhabdosomes of a larger form such as *P. typus* or *P. ilicifolius*. However, the apparent lack of a virgella, even in early growth stages, casts doubt on their identity with Hall's species.

Phyllograptus ilicifolius Hall 1858
Fig. 80a, b

1858 *Phyllograptus ilicifolius* J. Hall: 139.
1865 *Phyllograptus ilicifolius* Hall; Hall: 121–123; pl. 16, figs 1–9.

Lectotype. GSC 940, figured by Hall (1865: pl. 16, fig. 4) and refigured here (Fig. 80a), is here designated as **lectotype**. It is held by the Geological Survey of Canada.

Paratypes. GSC 940a–d, specimens figured by Hall (1865: pl. 16, figs 1–3, 5–9), and more than 20 other mature rhabdosomes in the same slabs, of which one is figured here, Fig. 80b. All held by the Geological Survey of Canada.

Stratigraphic horizon. Raymond (1914) and Bulman (unpublished MS) list the species from Zones A and C1–3, and Bulman further records it in Zone B, with *Phyllograptus typus*.

Discussion. The new information from the Spitsbergen phyllograptoids has made it necessary to re-examine the type series of *P. ilicifolius*. From material here figured it is apparent that the species bears close resemblance to *Phyllograptus typus*. Most significant is the fact that a true *Phyllograptus* rhabdosome structure can be determined from the type specimens, which are preserved in slight relief. One incomplete specimen lies on the edge of the slab containing the specimen of Hall's (1865) pl. 16, fig. 9. The edge of the slab was ground back to reveal a cross section of the rhabdosome, and the isolated central cruciform columella was clearly seen. Several other specimens, such as that figured in Fig. 80b, are preserved so as to expose the double row of fornical foramina. The evidence thus conflicts with Hall's own (1865: pl. 16, fig. 10) interpretation of rhabdosome structure which appears to be based on *Pseudophyllograptus* rather than *Phyllograptus, sensu stricto.*

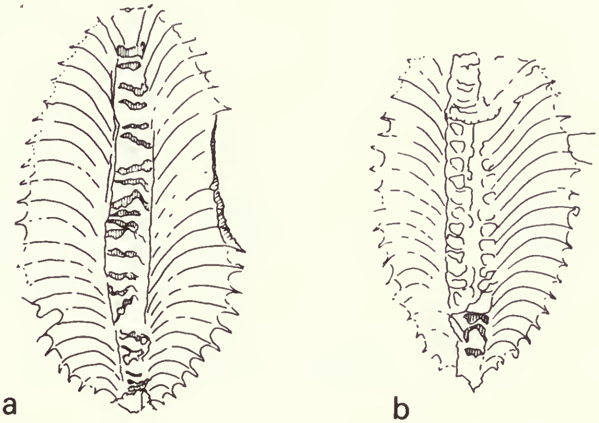

Fig. 80 *Phyllograptus ilicifolius* Hall, type series. a, **lectotype** GSC 940, original of Hall (1865: pl. 16, fig. 14). b, GSC 940c, specimen on slab with that figured by Hall (1865: pl. 16, fig. 9), showing double row of fornical foramina. Both × 3.

In a few specimens (Fig. 80b) the proximal end is well enough exposed to reveal a blunt sicular spine and the reclined attitude of the initial thecae is clearly seen in many specimens. There is no doubt that the species is a true *Phyllograptus*.

Thecae have a low initial angle of inclination, as in *typus,* and are strongly curved in the proximal region. Thecal spacing (12–16 in 10 mm, Fig. 81) is slightly closer than in Hall's *typus* but shows a similar, wide, range. The chief distinctions from Hall's *typus* are the lack of a prominent sicular spine (even in similar-sized rhabdosomes), a less tapered proximal rhabdosome outline and an apparently smaller maximum rhabdosome size. It may be argued that these are insufficient to maintain it as a distinct species, but it seems best to retain *P. ilicifolius* until population studies can clarify its distinctness or otherwise from *P. typus* at Levis. There is no doubt that the two forms are closely related. It is clear, from examination of the literature, that there has been much confusion in distinguishing between the two species, and a careful examination of specimens is needed before synonymy can be attempted.

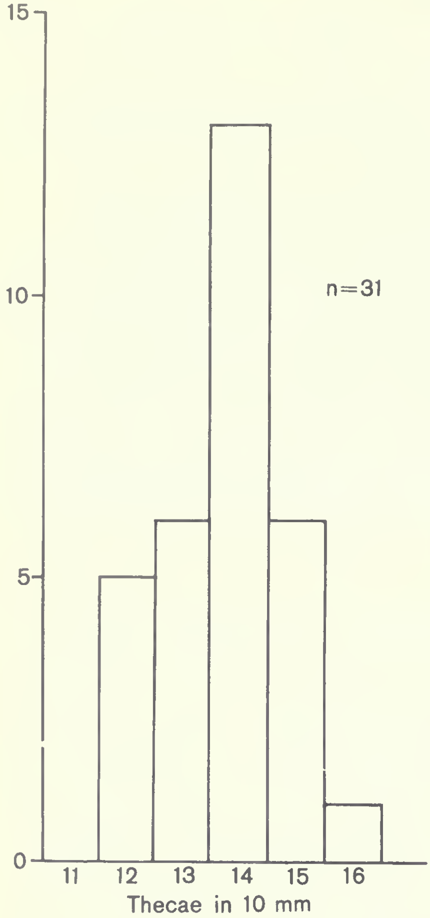

Fig. 81 *Phyllograptus ilicifolius* Hall, type series. Frequency distribution of thecal spacing (taken to nearest whole number).

Phyllograptus ? sp. nov.
Fig. 82

Stratigraphic range. 17–25 m level, Olendisletta Member, V_1b.

Material. PMO NF2047, NF3183.

Description and discussion. Although represented only by poorly preserved or incomplete material, the species is distinguished by the extremely close spacing of its thecae. Distally, thecal spacing is wider and measures about 4 in 2·5 m (equivalent to 16 in 10 mm). All rhabdosomes are very small (less than 12 mm long) and can be compared only with the proximal portions of other species such as *Phyllograptus anna,* from which they can be seen to differ in the closer spacing of their thecae.

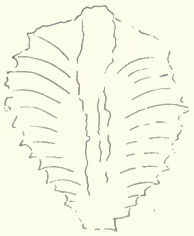

Fig. 82 *Phyllograptus*? sp. nov. PMO NF2047; small rhabdosome with closely spaced thecae. 25 m above base of Olenidsletta Member, southern section; × 4.

Although there appears to be no available name for the species, the poor preservation of our material precludes formalizing it as a new species. It may well be represented elsewhere in the world by those specimens, currently attributed to *Phyllograptus anna,* with a thecal count of 16–20 (e.g. Ruedemann 1947: 316 or *P. elegans* Ge (*in* Mu *et al.* 1979)). Internal rhabdosome structure is uncertain but from NF3183, in relief, appears likely to be that of *Phyllograptus* rather than *Pseudophyllograptus.*

Genus *XIPHOGRAPTUS* nov.

Type species. *Didymograptus formosus* Bulman 1936*a.*

Diagnosis. Phyllograptines having extensiform or declined didymograptid rhabdosome habit. Small growth stages show long, slender virgellar spine, and antivirgellar origin of th1^1. Sicula short, about 1·5 mm or less. Proximal stipe width narrow, with low thecal inclination.

Name. Ξιφος, 'a sword', referring to the virgellar spine occurring in all species.

Species included. *Didymograptus formosus formosus* Bulman 1936*a, D. formosus svalbardensis* Archer & Fortey 1974 (= *D. delicatus* Braithwaite 1976), *D. elongatus* Harris & Thomas 1940, and *D. 'nitidus', sensu* Braithwaite 1976; ?*D. patulus, sensu* Törnquist 1901 (*non* Hall 1865) (= *D. patulentis* Chen *in* Mu *et al.* 1979), ?*D. cypselo* Archer & Fortey 1974.

Discussion. The genus *Xiphograptus* is proposed for a number of species which would have formerly been regarded as extensiform *Didymograptus.* The struture of the proximal end shows that these species are more closely related to true *Phyllograptus* (but not to *Pseudophyllograptus*) as re-evaluated in this paper than to any of the *Didymograptus (Expansograptus)* group. We regard the extensiform rhabdosome habit as having been independently derived. The alternative is that the proximal end structure of *Phyllograptus* and *Xiphograptus* was independently arrived at, which seems most unlikely.

It requires reasonably well preserved material to see the characteristic virgellar spine which would betray a species as belonging to *Xiphograptus* rather than *Didymograptus (Expansograptus),* but the spine is visible in favourably preserved flattened material. It is probable that a number of previously-described species will ultimately prove to belong to the new genus. If, during astogeny, the virgellar spine comes to lie along the ventral margin of one of the stipes it will be necessary to have growth stages to determine that the species belong in *Xiphograptus.* From the species that we can already assign with confidence to *Xiphograptus* the stratigraphic range of the genus extends through the Arenig to the Llanvirn. So far, its distribution seems to be predominantly through the Pacific Province, like *Phyllograptus, sensu stricto.*

? *Xiphograptus elongatus* (Harris & Thomas 1940)

Fig. 83a–c; Pl. 1, fig. 11

?1940 *Didymograptus elongatus* Harris & Thomas: 132–133; pl. 1, fig. 12A; pl. 2, figs 14A, B.

Stratigraphic range. Specimens attributable to this species have been recovered from 17 m to 49 m from base, V_1b, spanning the latest Bendigonian to Chewtonian.

Material. Isolated proximal ends PMO NF3814–5; specimens on the rock include PMO NF2836 and numerous proximal ends.

Description. This species can be recognized both from specimens preserved in shale, and from isolated, slightly flattened examples. In most details the species closely resembles *Xiphograptus formosus svalbardensis* from the upper part of the Olenidsletta Member (Archer & Fortey 1974). The sicula is short, 1·2 to 1·3 mm long, excluding a very short nema, and the virgella, 0·7 mm long in some examples. Its aperture is 0·35 mm across, and probably broadly elliptical. The dorsal side of the sicula is prolonged into a lip and slightly curved so that the angle between the aperture and the virgella is acute. Theca 1^1 begins very high up on the sicula, probably at the base of the prosicula, and the sicula and th1^1 grow down in tandem such that 0·7 mm of the pair projects above the dorsal wall of the stipe. At about 0·3 mm from the base

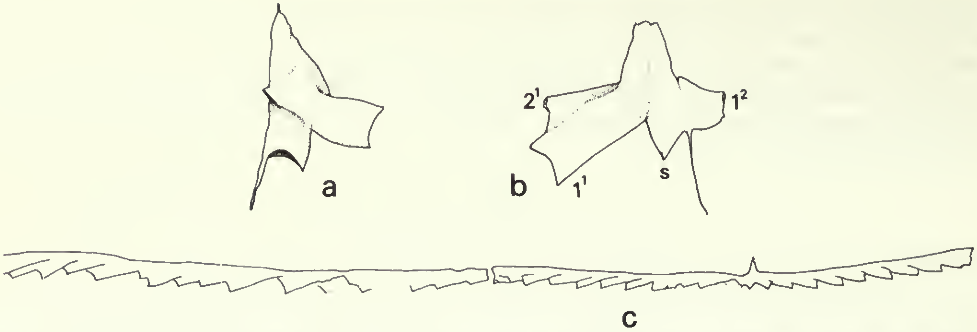

Fig. 83 ?*Xiphograptus elongatus* (Harris & Thomas), isolated, somewhat flattened growth stages and full rhabdosome. a, PMO NF3815, in reverse view showing 'hood' stage of development. b, NF3184, obverse view, showing long free ventral wall of th1^1. Both from 16 m above base of Olenidsletta Member on Profilstranda, × 18. c, NF2836, flattened, imperfect specimen, from 17 m above base of Olenidsletta Member, Olenidsletta; × 3.

of the sicula th1^1 takes a very sharp bend away from the sicula, such that the angle between the free wall of the sicula and the free ventral wall of th1^1 is 85°–90°. The distal part of th1^1 beyond the bend is 0·8 mm or slightly more. At the stage of production of th1^2 and th2^1 there is a characteristic 'hood' as shown by *D. formosus svalbardensis* (Archer & Fortey 1974: fig. 4a). Development isograptid: th1^2 and th2^1 subsequently grow out horizontally, and a horizontal to slightly reclined habit appears to characterize all the specimens from Spitsbergen. Dorsoventral stipe width at the level of the first thecae is 0·7 mm, and the maximum stipe width we have observed is 1·4 mm, with the increase being gradual in the manner of *D. extensus* (but with even lower gradient of increase). There is every reason to suppose that the stipes continued to grow and expand in width to the 2 mm mentioned as a maximum by Harris & Thomas. Thecal inclination remains low, about 20° even distally, and this is what accounts for the exceptionally low thecal spacing, 8 or 9 per 10 mm distally. Apertures were probably minutely denticulate, and the apertural margins are at an approximate right angle to the free ventral thecal walls (may appear slightly acute or slightly obtuse).

Discussion. Harris & Thomas (1940) gave a somewhat perfunctory description of *'Didymograptus' elongatus* from the Bendigonian of Australia. Nonetheless their figure (1940: pl. 2, fig. 14B) clearly shows the virgella, and the long free ventral wall of th1^1; the very narrow stipes, their slow expansion, consistently low thecal inclination and wide distal thecal spacing are all similar on our material and that of the Australian form. But we retain a caution in our determination. The similarity to the younger species *Xiphograptus formosus svalbardensis* (Archer & Fortey 1974) is obvious. Proximal ends are distinguished by several small details: the outward bend on th1^1 is sharper on *X. elongatus,* so that the angle between the free part of the sicula and that of th1^1 is generally larger, and the length of the free ventral wall of th1^1 is longer on the older species. Large populations of isolated specimens of *X. formosus svalbardensis* show a variation in this length between 0·4 and 0·6 mm, with the majority of specimens 0·5 mm, whereas we have 0·8 to 0·9 mm for this measurement on *X. elongatus.* Thecal inclination is probably even lower on *X. elongatus,* which accounts for its extremely loose thecal spacing distally, fewer thecae per 10 mm than *X. formosus svalbardensis.* Our populations of *X. elongatus* include only specimens with horizontal to slightly reclined stipes, whereas *X. formosus svalbardensis* includes a proportion of declined forms. However, with very thin stipes such differences should be viewed with caution in flattened material. *X. formosus formosus* (Bulman 1936*a*, Skevington 1965) has consistently more strongly declined stipes, and the virgella becomes virtually incorporated in the exterior wall of th1^2. It is possible that there is continuous intergradation between *X. elongatus, X. formosus svalbardensis* and *X. formosus formosus* through the Arenig.

Harris & Thomas (1940: 132) remark that the sicula in their specimens was 'apparently slightly inclined from normal to the axis of the stipes'. This appearance is common in flattened material, and is probably produced by a combination of the distal curvature of the sicula, with the antivirgellar origin of $th1^1$ and the broad crossing canal developed from the 'hood' leading to $th2^1$.

Xiphograptus formosus svalbardensis (Archer & Fortey 1974)

Pl. 1, figs 6–8

1974 *Didymograptus formosus svalbardensis* Archer & Fortey: 91–95, text-figs 3c–g, 4a–f.
1976 *Didymograptus extensus* (Hall), *s.s.*; Braithwaite: 48–49: pl. 9, figs 10, 11, 13.

STRATIGRAPHIC RANGE. Upper part of Olenidsletta Member, 116–130 m above base, V_3a–b, later Arenig (Castlemainian Ca_3 = lower part of *Isograptus* Zone).

ADDITIONAL MATERIAL. In addition to the original type material PMO NF3340–1 and NF3218 are figured here.

DISCUSSION. Archer & Fortey (1974) gave a full description of this species. Here we figure proximal ends to give a more detailed illustration of proximal structure for comparison with *X. elongatus*. There is a little more variation in this species than was allowed in the original description. Whole specimens may be horizontal, gently declined or reclined. Proximal stipe width at $th1^1$ may be as narrow as 0·55 mm (0·65 mm is usual) and distal stipe fragments may be as wide as 1·3 mm. One particularly interesting specimen (Pl. 1, fig 8) show distinctive prothecal folds, an extreme development of the small undulations which are often present on the dorsal wall of isolated specimens. But in other features this specimen is typical of *D. formosus svalbardensis* and there seems to be no reason why it should be regarded as a separate species. If it is not, it follows that the presence of prothecal folds ought not to be considered a fundamental character, and such folds may be capable of polyphyletic derivation.

Distinctions from *X. elongatus* are listed above. Braithwaite (1976) described *Didymograptus delicatus* from the early Ordovician of Utah; his illustrations of the proximal end (1976: pl. 16, fig. 6) demonstrate that this is a *Xiphograptus* species. Note that the virgellate sicula figured on Braithwaite's (1976) pl. 16, fig. 2 is also likely to belong to *Xiphograptus* rather than to *Didymograptus bifidus*. Variation in rhabdosome habit and thecal proportions are much like those of our species, but some specimens are stated to be much narrower at the proximal end (down to 0·32 mm), and at the population level this may indicate a specific distinction. Braithwaite gives the locality as from the Kanosh Shale: Archer & Fortey figured some Utah specimens from stratigraphically below this (shales beneath the Juab Limestone) which are undoubtedly conspecific with the Spitsbergen species, and of about the same age. This is probably what Braithwaite recorded as *D. extensus* (Hall). So *X. formosus svalbardensis* does occur in Utah, and may there extend into younger beds or be represented therein by closely related species. Braithwaite's *D. 'nitidus'* is another *Xiphograptus* altogether more robust than *X. formosus* subspp.

X. formosus svalbardensis is an extremely abundant species in the Spitsbergen Ordovician, and it would be surprising if it were not geographically widespread. It seems possible that some of the records of *D. extensus* from the younger Arenig may refer to this form. Some slender late Arenig didymograptids have been described with proportions not unlike those of the Spitsbergen species. For example *D. slemmestadi* Monsen 1937 appears to be generally similar, apart from slightly closer distal thecal spacing; Monsen indicates a normal dichograptid proximal end for this species (1937: pl. 2, fig. 10; also Mu *et al.* 1979: pl. 35, figs 22–24), and if this is correct it cannot be conspecific with the Spitsbergen form. A slender species of '*Didymograptus*' from the Arenig of New Zealand (Cooper 1979: pl. 12, fig. a) may also prove to be referable to this species.

Xiphograptus patulentis (Chen *in* Mu *et al.* 1979)

Pl. 1, figs 9, 10

1901 *Didymograptus patulus* (Hall); Törnquist: 15–17; pl. 2, figs 1–6.
1979 *Didymograptus patulentis* Chen *in* Mu *et al.*: 105–106; pl. 36, figs 5, 20, 21; pl. 37, fig. 1.

STRATIGRAPHIC RANGE. Upper part of Olenidsletta Member, 122 m from base, V_3b (upper Arenig, Castlemainian Ca_3).

MATERIAL. SM A105821–3.

DESCRIPTION. Only one specimen preserves a good proximal end. Stipes diverge at 180°, to become slightly reclined distally. Sicula about 1·8 mm long, with prominent virgella proving the assignment of this species to *Xiphograptus*. Stipe width at $th1^1$ is 1 mm, and the increase in stipe width is rapid, such that at the fourth or fifth theca it is 2 mm or more. Isolated stipes from the same bedding plane attain a width of 3 mm, a width that remains virtually constant over stipe lengths exceeding 3 cm. There seems to have been some variation in distal stipe width, but with proximal expansion rapid, much in the manner of *D. patulus*. Distal thecal spacing is exactly 10 thecae in 10 mm on available material. The 'cut away' appearance of the thecal apertures is characteristic, such that the free ventral thecal wall makes an angle of about 45° with the apertural profile. Thecal inclination distally 40°–50°.

DISCUSSION. Chen (*in* Mu *et al.* 1979) renamed the species described by Törnquist (1901) as *Didymograptus patulus* (Hall), noting that Törnquist's specimens differed in several respects from Hall's type material. We use the name *patulentis* Chen here, because our material compares closely with Törnquist's specimens, which are from the higher Arenig of Sweden (*D. patulus* is probably from the earlier Arenig). Törnquist's original description states 'In one specimen I have seen a filiform appendice projecting from the corner of the (sicular) aperture in every respect resembling the virgella . . .' This is a clear indication that Törnquist's specimens belong to *Xiphograptus*; Törnquist's (1901) pl. 2, fig. 4 shows isograptid development. Since *D. patulus* is apparently a normal *Didymograptus (Expansograptus)* it cannot be conspecific with the younger species from Sweden, nor with our material from Spitsbergen. Although Törnquist mentions a sicula as long as 3 mm his figures indicate a length of 2 mm or less, not greatly different from our material. Of specimens attributed to *D. patulentis* from south-west China only one (Mu *et al.* 1979: pl. 37, fig. 1) shows what is probably the virgella on the left of the sicula. There too the species occurs in high Arenig strata. The general growth of the stipes and the thecal form are very like *Didymograptus patulus,* but this must be a matter of parallel evolution. There has been the suggestion (e.g. Spjeldnaes 1953: 178) that *D. patulus* gave rise to *D. hirundo.* Spjeldnaes appears to refer to Törnquist's material in his account; since *hirundo* is as far as we can tell a normal *Didymograptus (Expansograptus), Xiphograptus patulentis* is not likely to be its ancestor.

Xiphograptus ? *cypselo* (Archer & Fortey 1974)

1974 *Didymograptus cypselo* Archer & Fortey: 89–91, text-figs 1, 3a, b.

STRATIGRAPHIC RANGE. Upper part of Olenidsletta Member, 116–130 m above base, V_3a, associated with *Pseudotrigonograptus minor* (late Arenig Ca_3).

REMARKS. There is nothing to add here to the description of Archer & Fortey (1974) except to note that the isolated proximal end (1974: 90) suggests that this species should now also be referred to *Xiphograptus.* The interpretation of that specimen may have been in error, with $th1^1$ lying on the antivirgellar side in the usual way for *Xiphograptus.* Since all the available specimens of *X. cypselo* have been secondarily greatly thickened interpretation of thecal order is difficult. The holotype is a specimen preserved on the rock, and because the virgellar spine has not been noted on that specimen, the attribution to *Xiphograptus* is tentative pending the recovery of more isolated material. The resorption of the sicula appears to be characteristic of *X.? cypselo,* but may be difficult to recognize in flattened material, and as with *X. formosus svalbardensis* there is the possibility of unrecognized synonyms in the literature.

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Plates 1–6

For reasons stated on p. 159, few of the Spitsbergen graptolites lend themselves readily to photography, except where they are in relief or where there is a natural colour contrast between the specimen and background. The photographs that follow are unretouched (except one example), and taken either under cold light or immersed in alcohol. Plate 1 is of wash drawings (R.A.F.) prepared at twice reproduction size. Photography by the Photographic Unit, British Museum (Natural History).

Definitions of Lower, Middle and Upper Arenig given for stratigraphic ranges are those defined on p. 168.

Accepted for publication 12 March 1982

Plate 1

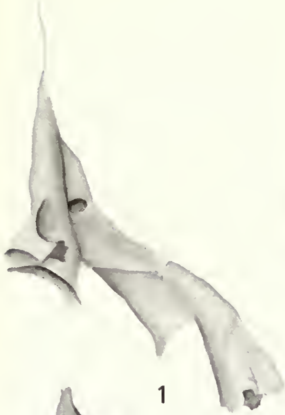
Wash drawings, mostly of isolated specimens.

Figs 1–5 *Didymograptus (Didymograptellus) multiplex* sp. nov., (p. 229). All isolated material from a high Middle Arenig horizon 91 m from base of Olenidsletta Member. Fig. 1, PMO NF3370, reverse view × 25. Specimen showing foramen from th1^1 into th1^2, part of which is preserved on the left. Periderm on right represents remains of aborted theca; th1^1 is dicalycal. Figs 2, 3, **Holotype** NF3369, reverse and obverse views respectively, × 25, showing aborted theca 2^1. Fig. 4, NF3371, most complete specimen, × 6, probably at isograptid stage. Fig. 5, NF3372, × 12. Proximal end slightly flattened, apparently at *artus* stage, but preservation may be inadequate to show aborted theca.

Figs 6–8 *Xiphograptus formosus svalbardensis* (Archer & Fortey), (p. 291). Upper Arenig. Fig. 6, NF3218, specimen on the rock × 3, showing general *'extensus'*-like appearance. 147 m from base of Olenidsletta Member. Fig. 7, NF3340, obverse view, × 25. 112 m from base of Olenidsletta Member on Profilstranda. Fig. 8, NF3341, reverse view × 25, same bed as Fig. 7. Shows distinct prothecal folds as an intraspecific variation.

Figs 9, 10 *Xiphograptus patulentis* (Chen *in* Mu *et al.*), (p. 292). Upper Arenig, specimens on the rock from 120 m from base of Olenidsletta Member on Profilstranda. Fig. 9, Part of SM A105822 × 6, detail from distal stipe having reached full width. Fig. 10, SM A105821 × 3, specimen with good virgellate proximal end.

Fig. 11 ?*Xiphograptus elongatus* (Harris & Thomas), (p. 289). Lower-Middle Arenig. Reconstruction × 25, based on specimens on the rock and isolated specimens drawn as Fig. 83, for comparison with *X. formosus svalbardensis* at same scale.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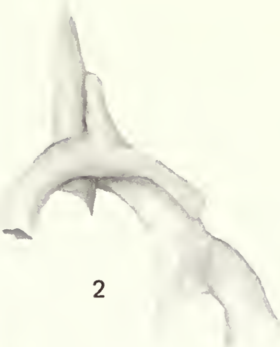
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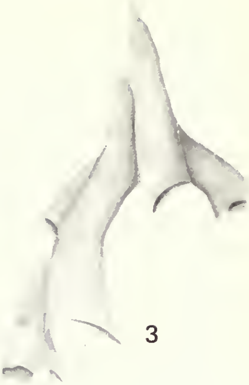
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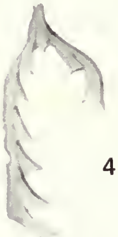
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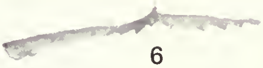
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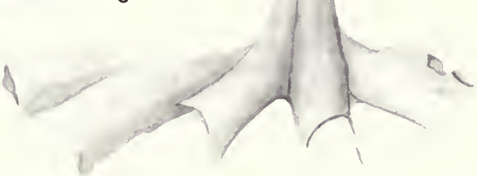
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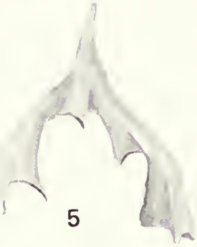
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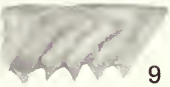
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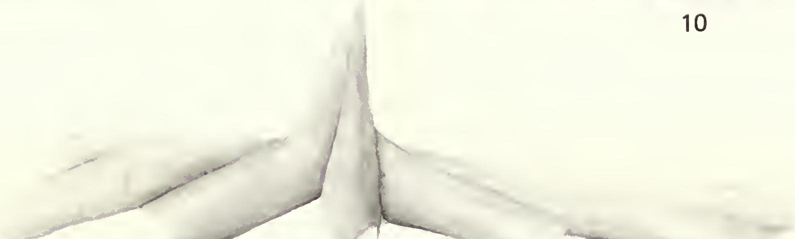
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Plate 2

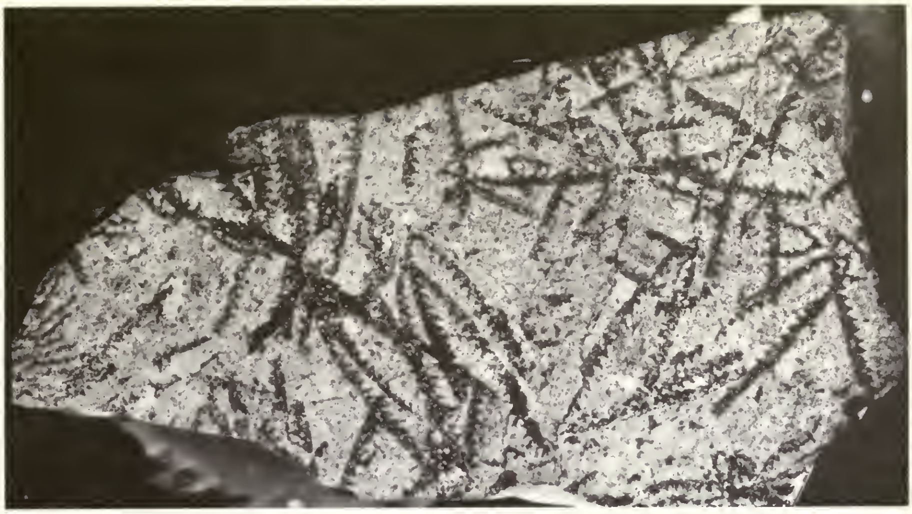
Fig. 1 *Didymograptus (Didymograptellus) 'protobifidus'* Elles, (p. 230). PMO NF1846 × 2. Slab covered with representative examples with relatively little intraspecific variation and near mean for species. Middle Arenig, Olenidsletta Member, Profilstranda, 45 m from base.

Fig. 2 *Clonograptus trochograptoides* Harris & Thomas, (p. 182). NF2795 natural size. Lower Arenig, low Olenidsletta Member on Olenidsletta, 22 m from base.

Fig. 3 *Dichograptus octobrachiatus* (Hall), (p. 188). NF3374 × 1. Representative large example with several small specimens. Lower Arenig, low Olenidsletta Member on Profilstranda.

Fig. 4 *Sigmagraptus crinitus* T. S. Hall, (p. 265). SM A105819 × 1. Lower Arenig, low Olenidsletta Member on Olenidsletta, 13 m from base.

Fig. 5 *Didymograptus v-fractus* Salter, (p. 239). NF3364 × 1·2. Lower Arenig, 13–20 m from base of Olenidsletta Member on Olenidsletta.



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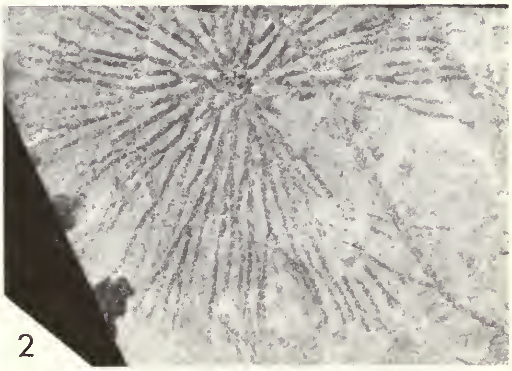

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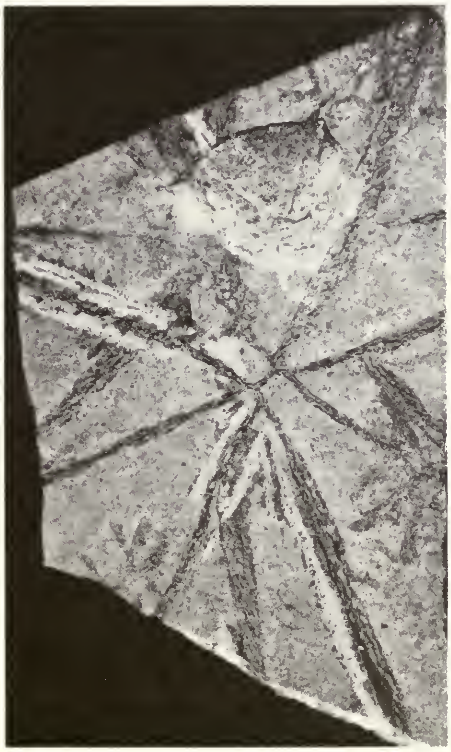

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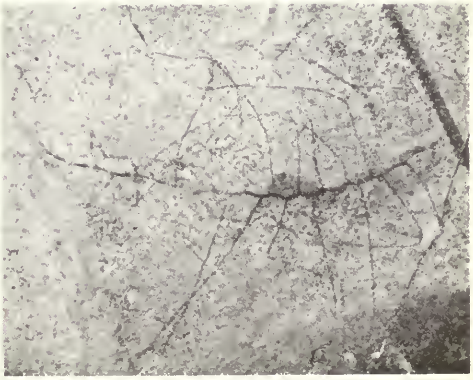

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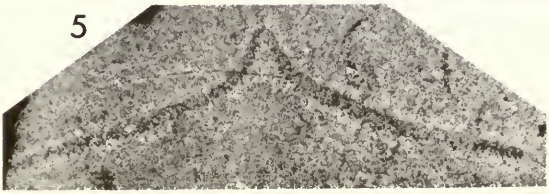

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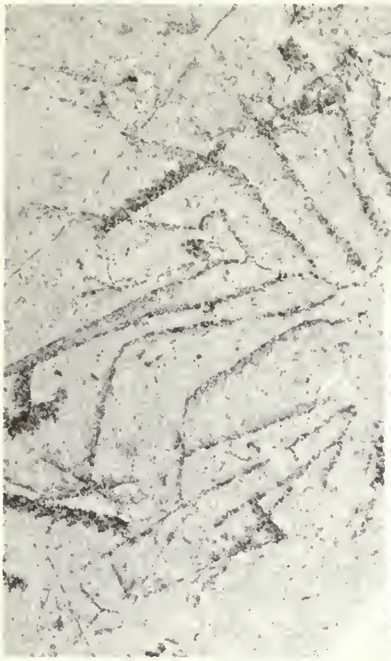
Plate 3

Fig. 1 *Goniograptus thureaui* M'Coy, (p. 266). SM A105820 × 2. Incomplete specimen but showing three of the four stipes. Lower Arenig, low Olenidsletta Member on Olenidsletta, about 4 m from base.

Figs 2, 3 *Tetragraptus contrarius* sp. nov., (p. 213). **Holotype,** NF2648. Flattened specimen showing three stipes. Fig. 2, × 1; Fig. 3, detail of proximal part showing characteristic stipe curvature, × 2. Middle Arenig, 90 m from base of Olenidsletta Member.

Fig. 4 *Tetragraptus fruticosus* (Hall), two-branched form (p. 210). NF3325 × 2. Lower Arenig, low Olenidsletta Member on Olenidsletta, 17 m from base.

Fig. 5 *Tetragraptus serra serra* (Brongniart), (p. 191). SM A105793 × 3. Representative example close to Brongniart's type. Lower Arenig, lower part of Olenidsletta Member on Olenidsletta.



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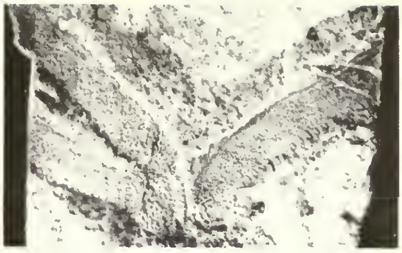

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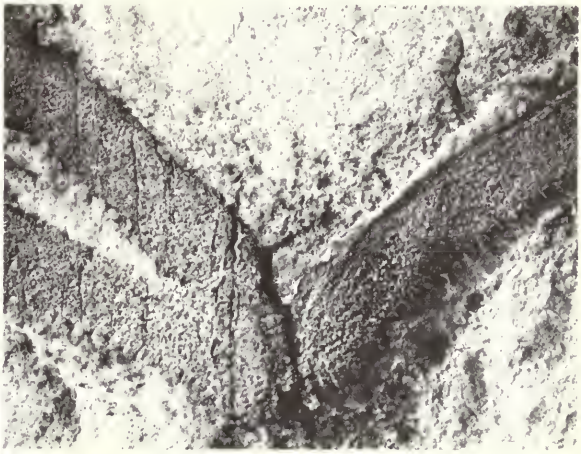

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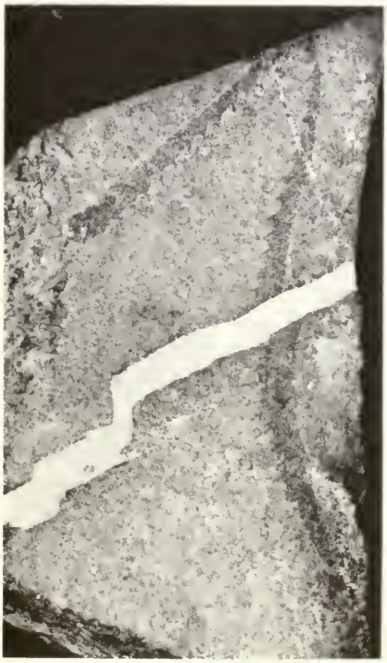

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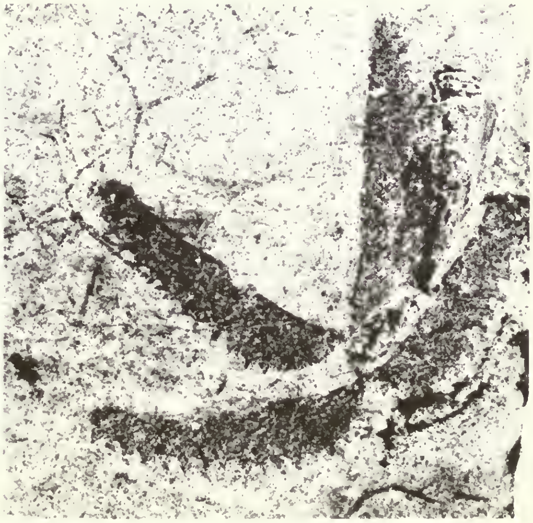

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Plate 4

Fig. 1 *Laxograptus irregularis* (Harris & Thomas), (p. 269). PMO NF3377 × 1 (retouched). Lower Arenig, Lower Part of Olenidsletta Member, 16 m from base.

Fig. 2 *Tetragraptus fruticosus* (Hall), three-branched, small form (p. 210). NF3378 × 1. Lower Arenig, lower part of Olenidsletta Member.

Fig. 3 *Tetragraptus phyllograptoides triumphans* subsp. nov., (p. 200). **Holotype** NF771 × 1. Specimen with sicula excavated; midpart of Olenidsletta Member, Middle Arenig, 75 m from base of Member.

Figs 4, 10 *Phyllograptus typus* (Hall), p. 274). Fig. 4, NF636 × 2. Typical relief rhabdosome with facing thecal series broken to show highly transverse bases of thecae. 75 m from base of Olenidsletta Member, Middle Arenig. Fig. 10, NF2046a × 2. Cluster of small rhabdosomes showing flat growing tops. 55 m from base of Olenidsletta Member, Middle Arenig.

Fig. 5 *Tetragraptus* cf. *Isograptoides* Gem (p. 199). NF1810 × 3. Two typical rhabdosomes of the youngest graptolite from Spitsbergen. Probably Llanvirn, shales at top of Profilbekken Member.

Fig. 6 *Pseudophyllograptus angustifolius chors* subsp. nov., (p. 244). **Holotype** NF1493 × 2. Base of Upper Arenig, 100 m from base of Olenidsletta Member on Profilstranda. Note more rectangular thecal bases of broken stipe compared with *Phyllograptus typus,* Plate 4, fig. 4.

Fig. 7 Form close to *Phyllograptus rotundatus* Monsen 1937, but which may be an extreme *P. typus* variant. SM A109732 × 3. See Fig. 70h, p. 278.

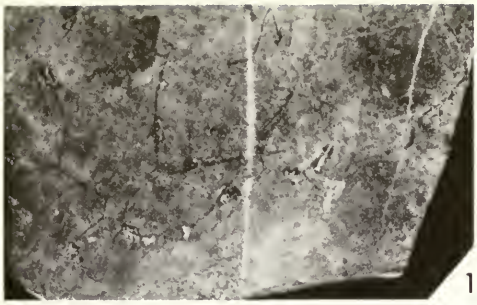
Fig. 8 *Pseudophyllograptus angustifolius* subsp. nov., (p. 247). NF3361 × 2. Lower Arenig, early Olenidsletta Member on Profilstranda, 8·6 m from base.

Fig. 9 *Didymograptus, sensu lato,* cf. *D. pennatulus* (Hall), (p. 240). NF3377 × 1. Two distal stipe fragments in relief. Upper Arenig, top part of Olenidsletta Member (V_3b) on Profilbekken.

Fig. 11 *Tetragraptus* cf. *reclinatus reclinatus,* (p. 205). NF2791 × 2. Lower Arenig, 22 m from base of Olenidsletta Member.

Fig. 12 *Didymograptus (Expansograptus) praenuntius* Törnquist, (p. 235). NF475 × 3, immersed in alcohol. Lower Arenig, lowest part of Olenidsletta Member on Profilstranda, transition beds with underlying Kirtonryggen Formation.

Figs 13, 14 *Tetragraptus quadribrachiatus* (J. Hall), (p. 216). × 2. Lower Arenig. Fig. 13, NF3319, 13 m above base of Olenidsletta Member. Fig. 14, NF3320, lower part of Olenidsletta Member.



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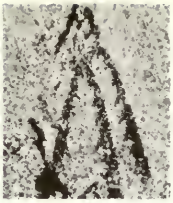

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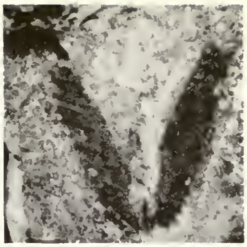

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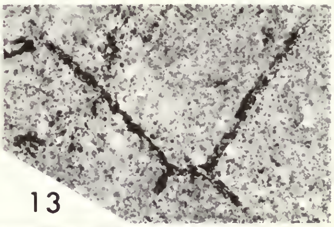

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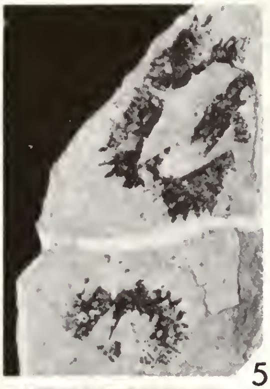

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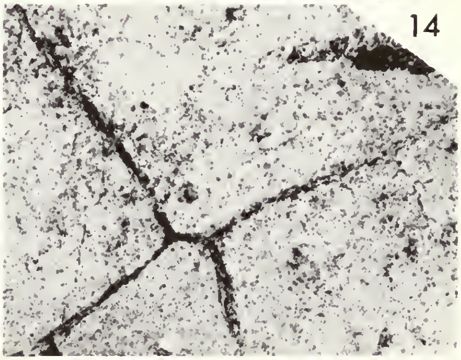

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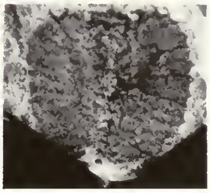

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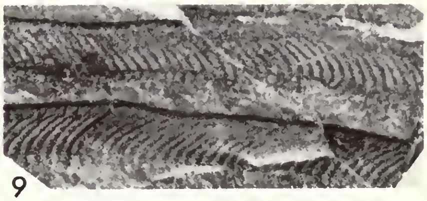

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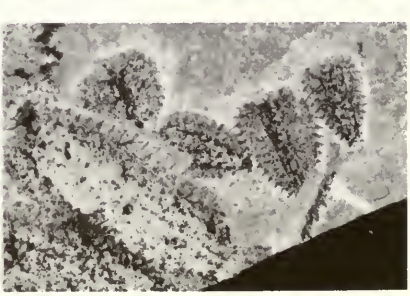

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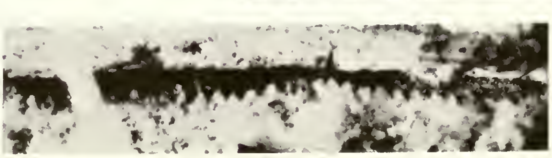

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Plate 5

Figs 1–3 *Isograptus scandens* sp. nov., (p. 257). × 6. Fig. 1, **Holotype** PMO NF3334. Showing long nema, and highly reclined stipes that do not touch back to back. Fig. 2, NF3380. The dorsal margins of the stipes have coalesced. Fig. 3, NF3379. Small growth stage. All Middle Arenig, isograptid bed, 49–50 m from base of Olenidsletta Member on Olenidsletta.

Figs 4, 5 *Didymograptus (Didymograptellus)* cf. *exilis* Ni, (p. 227). × 6. Fig. 4, NF3381. Fig. 5, NF3382. Both Middle Arenig, isograptid bed, 49–50 m from base of Olenidsletta Member on Olenidsletta.

Figs 6, 9 *Tetragraptus (Tetragraptus) amii* Lapworth, (p. 198). Fig. 6, NF3324 × 1. Two specimens shown, with specimen of *Isograptus scandens* on left. Middle Arenig, same bed as Plate 5, figs 4–5. Fig. 9, NF3324a × 6. Small specimen from same bed.

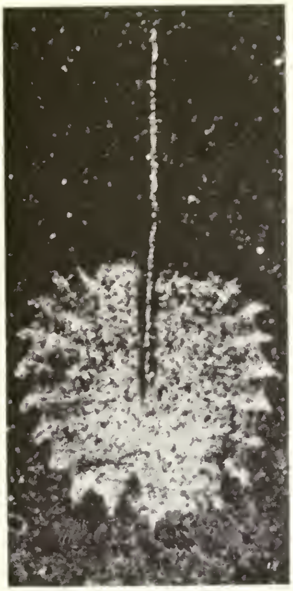
Fig. 7 *Tetragraptus (Tetragraptus) pseudobigsbyi* Skevington, (p. 202). NF433, relief specimen photographed under alcohol, × 3. Middle Arenig (upper part), 92 m from base of Olenidsletta Member on Profilstranda.

Fig. 8 *Tetragraptus (Tetragraptus) serra* (Brongniart) subsp. 1, large form, (p. 197). SM A105801 × 1. Lower Arenig, Olenidsletta Member, 11 m from base of Olenidsletta.

Fig. 10 *Isograptus victoriae victoriae* Harris, (p. 254). NF3385, relief specimen photographed under alcohol, × 3. Upper Arenig, 120 m from base of Profilbekken Member, Profilstranda.

Figs 11, 12 *Didymograptus (Didymograptellus) bifidus* (Hall), (p. 220). Fig. 11, NF2031 × 2. Slender, subparallel striped morph of this species. Middle Arenig (upper part), stream E on Olenidsletta, about 85 m from base of Member. Fig. 12, NF621, proximal part of relief specimen under alcohol, × 3. Middle Arenig, 75 m from base of Member on Profilstranda, same horizon as typical *bifidus* in Fortey (1976: text-fig. 3).

Fig. 13 *Pseudotrigonograptus minor* Mu & Lee, (p. 250). NF3386 × 3. Rhabdosome preserved in relief to show thecal apertures, a view which has been mistaken for a biserial rhabdosome. For other photographic illustrations of this species from Spitsbergen see Fortey (1971: plate 29). Upper Arenig, 112 m from base of Olenidsletta Member on Profilstranda.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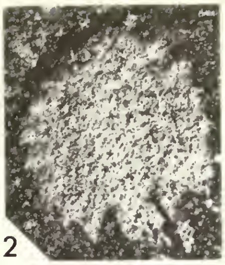
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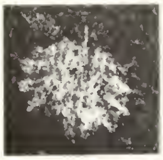
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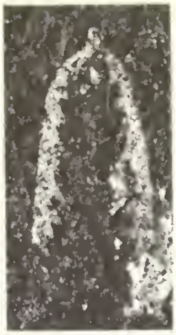
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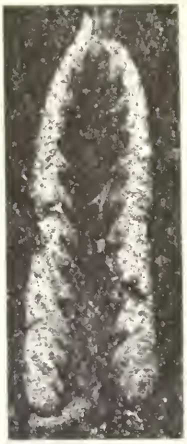
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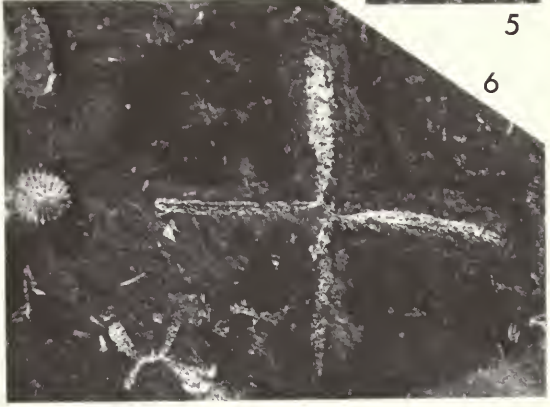
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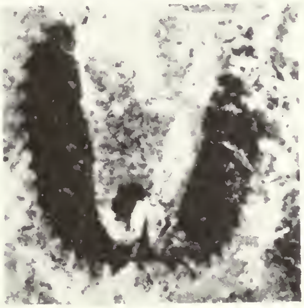
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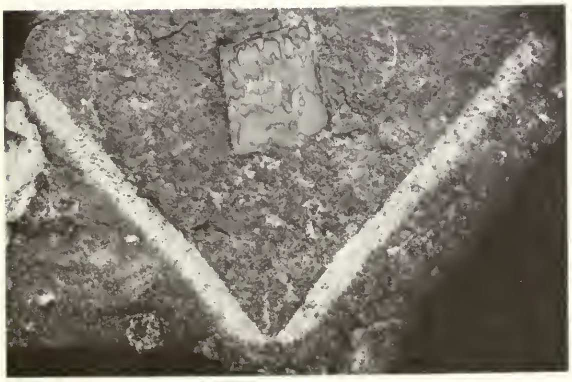
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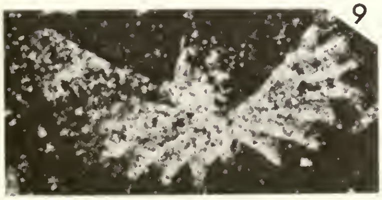
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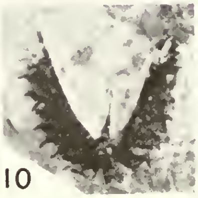
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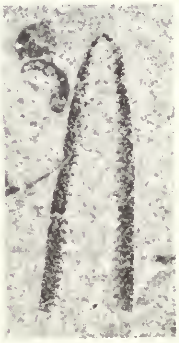
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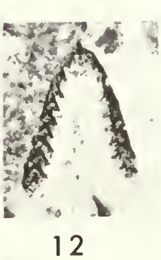
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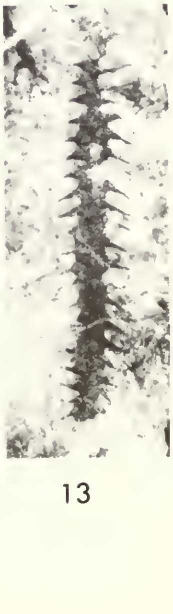
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Plate 6

Didymograptus (Expansograptus) extensus (Hall), (p. 231). SM A109727 × 1·5. Slab covered with representative examples of this species; arrows point to two proximal ends. Lower Arenig, low Olenidsletta Member on Olenidsletta, late Bendigonian interval about 17 m from base.

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Geology series
Vol **36** No 4 pp 303–332

British Museum (Natural History)
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Issued 23 December 1982

Campanian and Maastrichtian sphenodiscid ammonites from southern Nigeria

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Synopsis

Marine horizons in the Campanian–Maastrichtian Nkporo Shale of southern Nigeria are rich in sphenodiscid ammonites. Basal (Upper Campanian) strata yield *Libycoceras afikpoense* Reyment, which is succeeded by the Upper Campanian *L. crossense* sp. nov. and the uppermost Campanian to lowermost Maastrichtian *L. dandense* (Howarth). These species are part of an evolutionary lineage displaying rapid modification towards a *Sphenodiscus*-like morphology. True *Sphenodiscus* appears in the Nigerian Upper Campanian where *S. lobatus lobatus* (Tuomey) occurs infrequently. The ornamented *S. lobatus costatus* subsp. nov. is a Maastrichtian derivative of these earlier forms. Phylogenetic relationships within the family Sphenodiscidae are discussed. It appears probable that the family, as currently defined, is not monophyletic. It is necessary therefore to propose a new family, the Libycoceratidae, to include the genera *Libycoceras* and *Indoceras*.

Introduction

Ammonites of the family Sphenodiscidae have been known from Nigeria for some time. Reyment (1955, 1957) described species of *Libycoceras* and *Sphenodiscus* from southern Nigeria along with a member of the former genus from the north-east of the country. Kogbe (1979, 1980) also reported *Libycoceras* from north-western Nigeria. Reyment (1956, 1965) outlined a zonal scheme for the southern Nigerian Maastrichtian partly based on sphenodiscids. His zones were inferred from distant sections, highlighting a major problem in sphenodiscid taxonomy and phylogeny – the world-wide shortage of sections exhibiting reliable sphenodiscid successions. New material from southern Nigeria described here includes members of observable sphenodiscid lineages which provide valuable information on the age of certain genera and relationships within the family.

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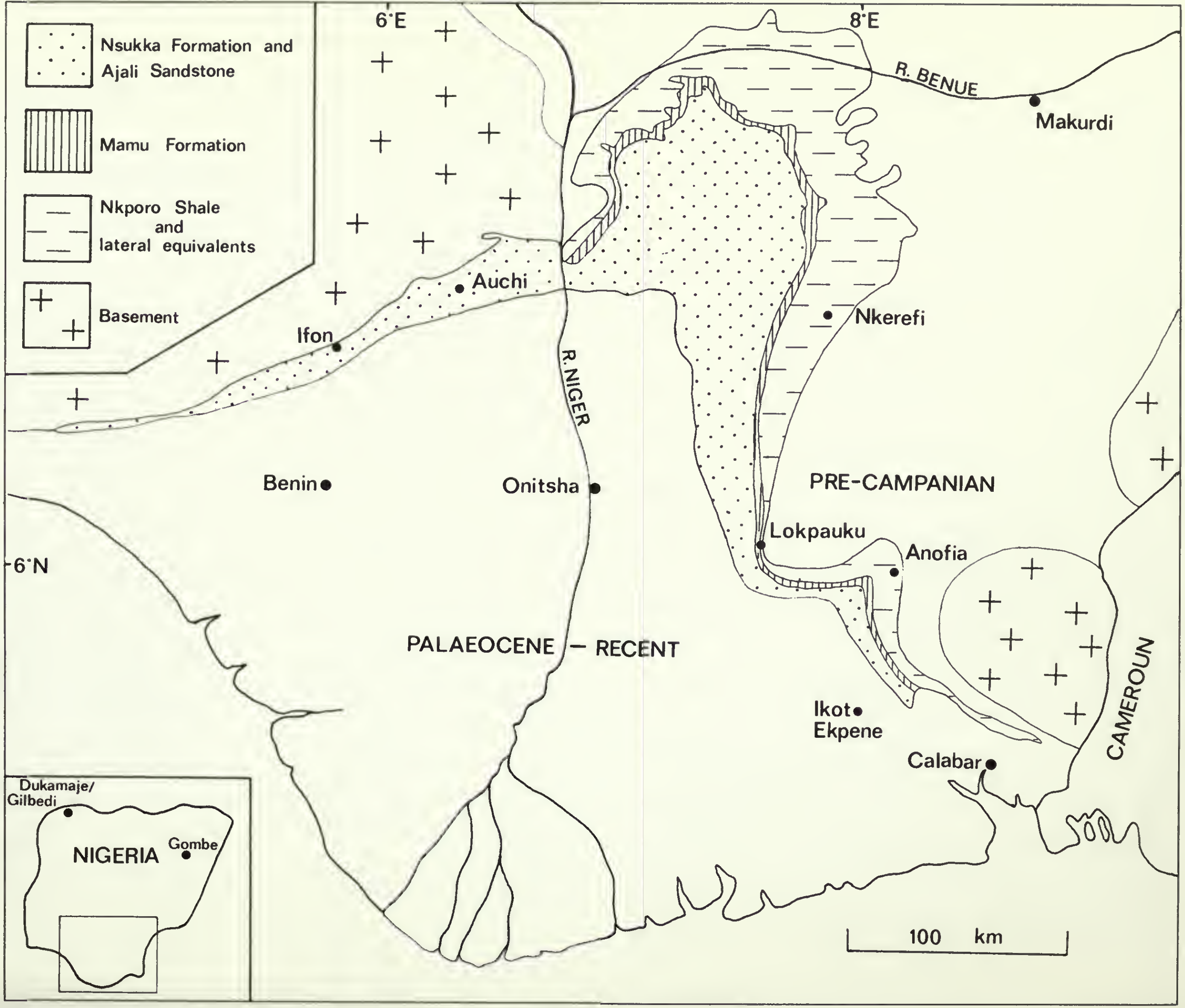

Nsukka Formation and Ajali Sandstone
Mamu Formation
Nkporo Shale and lateral equivalents
Basement
6°E
8°E
6°N
R. BENUE
Makurdi
Auchi
Ifon
R. NIGER
Nkerefi
PRE-CAMPANIAN
Benin
Onitsha
Lokpauku
Anofia
PALAEOCENE – RECENT
CAMEROUN
Ikot Ekpene
Calabar
100 km
Dukamaje/Gilbedi
NIGERIA
Gombe

Fig. 1 Map showing outcrops of Campanian and Maastrichtian formations in southern Nigeria and fossil localities mentioned in the text.

Occurrence of sphenodiscids in southern Nigeria

Most of the sphenodiscids from southern Nigeria previously described are from the Nkporo Shale, a Campanian–Maastrichtian formation outcropping in southern and central Nigeria (Fig. 1). In its lower part the Nkporo Shale is predominantly marine, but non-marine shales occur above. The marginal marine Enugu Shale and the Owelli (Awgu) Sandstone are lateral equivalents. Lying above and partly contemporaneous with the Nkporo Shale is a deltaic sequence comprising the coal-bearing Mamu Formation, the continental Ajali Sandstone and the paralic Nsukka Formation (in older literature the Lower Coal Measures, Falsebedded Sandstones and Upper Coal Measures respectively). Everywhere in south-eastern Nigeria the Nkporo Shale lies unconformably above a folded pre-Campanian sequence. Details of the stratigraphy can be found in Simpson (1954), Reyment (1956, 1965) and de Swardt & Casey (1961).

The most widely reported sphenodiscid of southern Nigeria is *Libycoceras afikpoense* Reyment, occurring in the Nkporo Shale and its lateral equivalents around Nkerefi and Anofia (Reyment 1955) and near Ngusu (Simpson 1954) between Lokpauku and Anofia (Fig. 1). Reyment (1956) reported it also from the basal Mamu Formation. Forms referred to *Sphenodiscus* aff. *lobatus* (Tuomey) and *S.* sp. indet. by Reyment (1955) occur in association with *L. afikpoense* at Anofia. The Nsukka Formation (?) near Ifon and Auchi (Fig. 1) contains *S. studeri* Reyment (Reyment 1955, 1957).

Knowledge of the Nkporo Shale ammonite faunas has been restricted by the scarcity of exposures and the impersistence both laterally and vertically of marine strata. Recently, however, roadworks have created excellent exposures in parts of southern Nigeria. In particular, cuttings on the Calabar–Ikot Ekpene road in the extreme south-east (Fig. 2) provide the opportunity to study a sequence of exposures through the formation. Here the Nkporo Shale lies uncomformably upon the Albian to Turonian Odukpani Formation. The mileposts provide

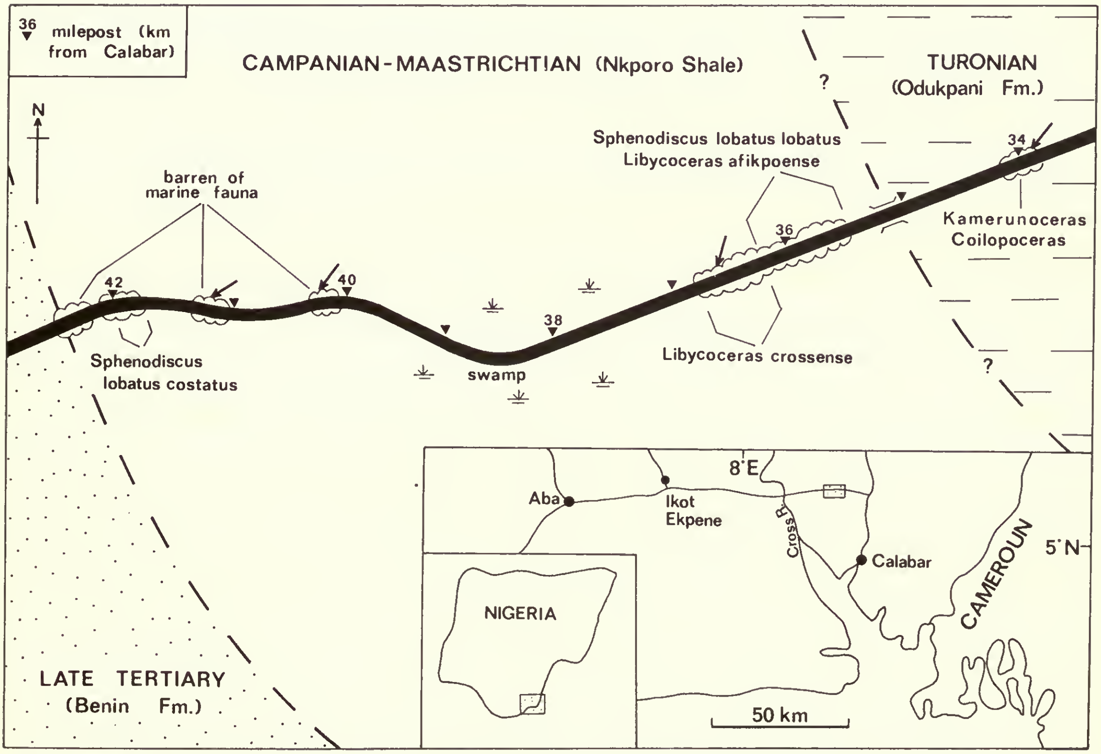

36 milepost (km from Calabar)
CAMPANIAN-MAASTRICHTIAN (Nkporo Shale)
TURONIAN (Odukpani Fm.)
N
?
Sphenodiscus lobatus lobatus
Libycoceras afikpoense
34
barren of marine fauna
36
Kamerunoceras
Coilopoceras
42
40
38
Sphenodiscus lobatus costatus
swamp
Libycoceras crossense
?
LATE TERTIARY (Benin Fm.)
8°E
Aba
Ikot Ekpene
Cross R.
Calabar
5°N
CAMEROUN
NIGERIA
50 km

Fig. 2 Map showing occurrences of ammonites in the Nkporo Shale north-west of Calabar.

good reference points. At 34 km from Calabar limestones of the uppermost Odukpani Formation yield *Coilopoceras* and *Kamerunoceras*. Between here and 35·5 km from Calabar occurs the concealed contact with the Nkporo Shale, which dips at *c.* 7°–8° to the south-west. Around the 36 km post, about 70 m of dark grey shales with interbedded thin shelly limestones and cross-bedded calcarenites are exposed. This is the basal Nkporo Shale in which *Libycoceras afikpoense* abounds. In addition *Sphenodiscus lobatus lobatus* (Tuomey) occurs occasionally, being most frequent towards the top of the range of *L. afikpoense*. A rich associated fauna includes *Gaudryceras* sp., *Pachydiscus* sp., *Baculites* sp., *Didymoceras* spp. and *Solenoceras* sp. *L. afikpoense* persists in numbers up through the sequence until about 36·3 km from Calabar, where it gives way to *L. crossense* sp. nov., which in turn ranges up through the next 45 m of shales. Its associated fauna is sparse, including a few *Inoceramus* and vertebrate fragments and rare *Nostoceras*? sp. Within the range of *L. crossense* the limestone bands die out and thin ironstone bands and nodules appear. These lithological changes and the faunal reduction probably herald the onset of reduced salinity conditions. Further cuttings are absent until 40·3 km and 41 km from Calabar where dark grey shales with ironstones occur, which are barren except for plant remains and rare vertebrate fragments. These are probably non-marine horizons. At 42 km from Calabar, about 40 m below the unconformable contact of the Nkporo Shale with the overlying late Tertiary Benin Formation, a rich marine fauna occurs again, preserved mainly in calcareous nodules distributed through 10–15 m of shales. *Sphenodiscus lobatus costatus* subsp. nov. is highly abundant here, and frequent *Pachydiscus (P.)* aff. *dossantosi* (Maury) and *P. (Neodesmoceras)* sp. along with rarer *Baculites* sp. also occur. The crab *Costacopluma* is common and the foraminifer *Afrobolivina* abounds. The Benin Formation oversteps the Cretaceous formations in this region and the uppermost part of the Nkporo Shale is possibly concealed. The outcropping part of the Nkporo Shale is *c.* 700 m thick.

At Lokpauku, some 130 km to the north-east of Calabar (Fig. 1), the Nkporo Shale is again exposed in road cuttings in the core of a broad anticline. For about 35 m below the gradual contact with the overlying Mamu Formation (see Simpson 1954: fig. 4) the Nkporo Shale yields only the crab *Costacopluma*. Below this two marine bands occur, each about 2 m thick, and separated by 6 m of ripple-bedded and laminated fine-grained sandstones. These bands yield numerous *Libycoceras dandense* (Howarth) and a single *Polyptychoceras*? has also been recovered. There is abundant plant matter, these shales probably being of a marginal marine nature.

The stratigraphical relationship between the Calabar and Lokpauku sections is shown in Fig. 3.

Systematic descriptions

Repositories. Repositories of specimens are identified by the following prefixes: UIN, Department of Geology, University of Ilorin, Nigeria; USNM, United States Museum of Natural History, Ithaca, New York. The remainder of the material is in the British Museum (Natural History), London, the catalogue numbers being prefixed by the letter C.

Dimensions. Much of the material is from shales and is compressed; only accurately determined dimensions are listed.

Superfamily **ACANTHOCERATACEAE** Hyatt

Family **LIBYCOCERATIDAE** nov.

The genera *Libycoceras* and *Indoceras* have previously been grouped with *Sphenodiscus* and related forms within the family Sphenodiscidae. The present material, however, suggests that *Libycoceras, Indoceras* and probably several other forms were derived separately (see 'Interrelationships within the family Sphenodiscidae', p. 323). It is necessary, therefore, to separate *Libycoceras* and *Indoceras* from *Sphenodiscus* taxonomically and the family Libycoceratidae is proposed for their reception. This family includes involute, compressed

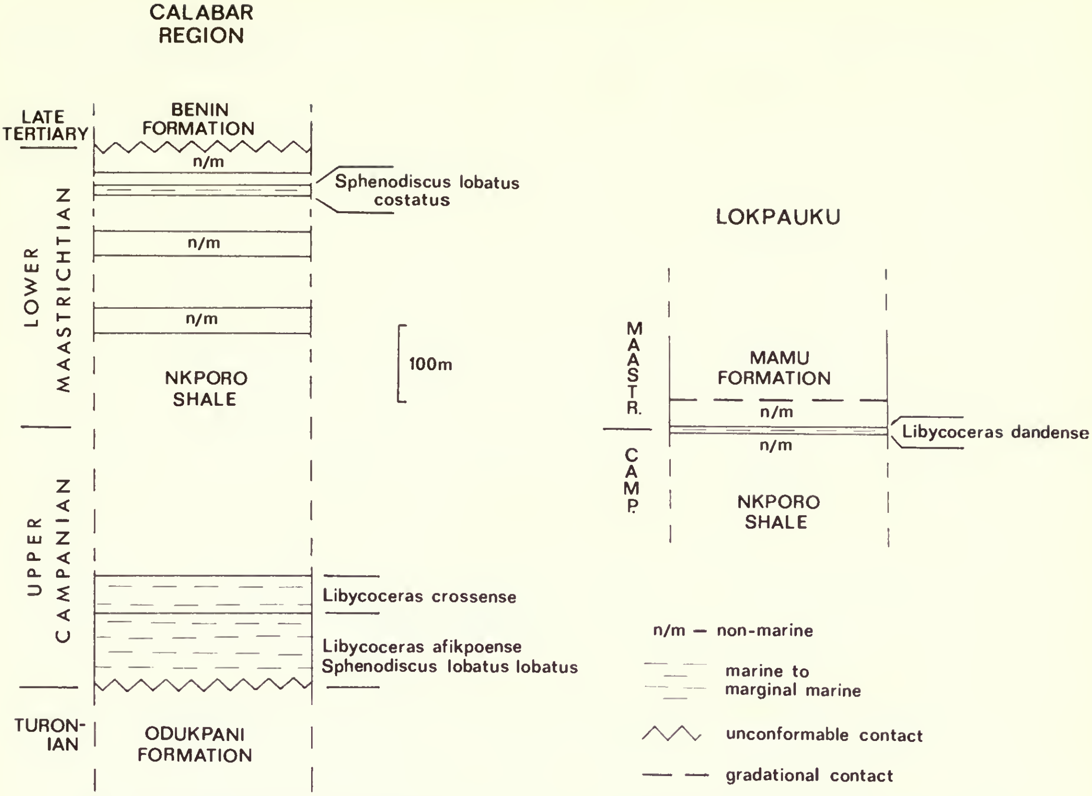

CALABAR REGION
LATE TERTIARY
BENIN FORMATION
n/m
Sphenodiscus lobatus costatus
LOWER MAASTRICHTIAN
n/m
n/m
NKPORO SHALE
100m
UPPER CAMPANIAN
Libycoceras crossense
Libycoceras afikpoense
Sphenodiscus lobatus lobatus
TURONIAN
ODUKPANI FORMATION
LOKPAUKU
MAASTR.
CAMP.
MAMU FORMATION
n/m
n/m
Libycoceras dandense
NKPORO SHALE
n/m — non-marine
marine to marginal marine
unconformable contact
gradational contact

Fig. 3 Stratigraphical relationships of the Nkporo Shale in the Calabar and Lokpauku areas.

ammonites with or without pronounced mediolateral and ventrolateral tubercles or rib-like ornament. The venter is tabulate to sharply rounded in the adult. The sutures have wide to narrow-necked saddles which are entire to moderately frilled. The first lateral saddle is divided by one or two adventitious lobes.

Genus *LIBYCOCERAS* Hyatt, 1900

TYPE SPECIES. *Sphenodiscus ismaelis* Zittel 1884. Upper Campanian; Middle East, North Africa, Sahara.

DISCUSSION. Howarth (1965: 394) has revised the genus *Libycoceras*, rejecting the older diagnoses of Picard (1929), Hourcq (1949) and Basse (1954) in which only forms with a bifid first lateral saddle (S_1) were included. Howarth included both *'Sphenodiscus' acutodorsatum* Noetling and *Paciceras* Olsson in *Libycoceras*, although they exhibit secondary trifurcation of S_1 (Noetling 1897: pl. 21, fig. 3a; Olsson 1944: fig. 3). The material referred here to *L. crossense* and *L. dandense* shows primary trifurcation of S_1. The former species shows a gross morphology and ornamentation typical of *Libycoceras*. The latter shows an ornament of a reduced but similar type and is probably derived from the former. Placing these species elsewhere on the basis of suture pattern alone would only serve to obscure their phylogeny.

Apart from these species mentioned above, four others are recognized, all showing a bifid S_1 with all saddles usually entire though the outer ones may be weakly indented (Lewy 1977: fig. 3). These species are *L. chargense* Blanckenhorn, *L. angolense* Haughton, *L. ismaelis* (Zittel) and

L. afikpoense Reyment. *L. chargense* retains a sharp venter throughout ontogeny and is usually smooth (Blanckenhorn 1900, Douvillé 1928) though Reyment (1955: 90) noticed faint ventrolateral tubercles. *L. angolense* is said to lack mediolateral tubercles (Haughton 1925: 270). *L. ismaelis* and *afikpoense* have a similar ornament of mediolateral and ventrolateral tubercles (Quaas 1903, Reyment 1955) and are distinguished mainly on the basis of venter breadth. The venter is generally narrower in *L. ismaelis*, especially in the adult stages. *L. ismaelis* occurs widely in North Africa, the Middle East and the Sahara (Quaas 1903, Picard 1929, Pérébaskine 1930, Collignon 1957, 1965, Sornay 1959, Lewy 1977). The Middle East populations show a considerable variation in breadth of venter and strength of ornament. Lewy (1977) figured examples with gross morphologies ranging from a *L. chargense*- to a *L. afikpoense*-like form. These ammonites inhabited partly isolated basins (Reiss 1962, Lewy 1977) and it is quite possible that excessive taxonomic splitting of variable, geographically separated populations has taken place. *L. ismaelis* and *L. afikpoense* remain difficult to distinguish, although the former sometimes seems to display a greater number of auxiliary saddles in the suture (Quaas 1903: pl. 29, fig. 6; Lewy 1977: fig. 3) than *L. afikpoense*, which normally shows four even in the adult stages. In gross morphology *L. angolense* resembles *L. ismaelis*, particularly in its narrow venter. Probably all four of these species are very closely related and are geographical variants of a common stock.

Specimens referred to *Coahuilites* by Lewy (1977: 249; pl. 1, figs 7–8) do not seem to be closely related to that genus, which has a considerably more complex suture pattern (Böse 1927). Instead, they resemble *L. crossense* in ornament and in the tendency towards secondary trifurcation of S_1. Individuals from Senegal, referred by Sornay & Tessier (1949) to *Daradiceras* and *Sphenodiscus corroyi*, are also probably closely related to *L. crossense*, as is '*S.*' *spathi* Picard (1929).

In the Middle East, the beginning of the range of *Libycoceras* has been accurately dated. Here *L. ismaelis* is of Upper Campanian age, occurring in the Zone of *Bostrychoceras polyplocum* (Reiss 1962). In one area *L. ismaelis* occurs associated with *Sphenodiscus* (Picard 1929, Lewy 1977). The same *Libycoceras–Sphenodiscus* association occurs in the basal Nkporo Shale. *L. afikpoense* in Nigeria is also very probably of Upper Campanian age, especially considering its close resemblance to *L. ismaelis*. *L. crossense* is slightly younger than *L. afikpoense*, being probably of late Upper Campanian age.

The genus *Libycoceras* seems to have possessed a certain tolerance of abnormal marine conditions. This is so in the Middle East (Reiss 1962, Lewy 1977), and the persistence of *L. crossense* in the Nkporo Shale around Calabar, while the rest of the marine fauna dies out, is further evidence of this.

Libycoceras afikpoense Reyment, 1955
Figs 4, 7, 8, 10, 14

? 1954 *Libycoceras ismaelis* (Zittel); Simpson: 13.
? 1954 *Libycoceras angolense* Haughton; Simpson: 17.
1954 *Libycoceras ismaelis* (Zittel); Reyment: 21.
1955 *Libycoceras afikpoense* Reyment: 89–90; pl. 21, figs 1, 2a, 2b; pl. 22, figs 6a, 6b; pl. 23, fig. 2.
? 1955 *Libycoceras* sp. juv. Reyment: 90; pl. 19, fig. 3; pl. 20, fig. 4.
1965 *Libycoceras afikpoense* Reyment; Reyment: 55, 56; pl. 2, fig. 10; pl. 6, fig. 6.

MATERIAL AND OCCURRENCE. The present material consists of 237 specimens (UIN 423.1–423.228; C.83130–C.83137, C.83230) from the lowermost Nkporo Shale (Upper Campanian), around 36 km from Calabar on the Calabar–Ikot Ekpene road, south-eastern Nigeria. The species occurs in the Upper Campanian of various parts of southern Nigeria as far north as Nkerefi (Simpson 1954, Reyment 1955, 1956). The holotype (C.47403) and three paratypes (C.47404, C.47405, C.47416) were among the material described by Reyment (1955). Specimens described by Lewy (1977) are probably variants of the closely related *L. ismaelis*.

Dimensions. In mm. D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter. Figures in parentheses are dimensions as a percentage of the total diameter.

	D	*Wb*	*Wh*	*U*
UIN 423.1	—	30	55	8
	50	14 (28)	31 (62)	—
	31	8 (26)	18 (58)	—
	21	5·3 (25)	13 (62)	—
	12	2·8 (23)	8 (66)	—
C.83135	83	23 (28)	45 (54)	7 (8)
	60	18 (30)	33 (55)	5 (8)
	42	11 (26)	22 (52)	3 (7)
UIN 423.2	59	15 (25)	33 (56)	5 (8)
UIN 423.3	60	15 (25)	33 (55)	5 (8)
C.83230	77	23 (30)	43 (56)	—
	58	16 (28)	34 (59)	—
	28	6 (21)	16 (57)	—
	5	1 (20)	3 (60)	—
	—	1	1·5	—

Description. Although this species has been described by Reyment (1955) it is desirable to include an account of the present material for the purposes of clarity and completeness.

The shell attains a diameter in excess of 120 mm, the body chamber being a little less than half a whorl in length. Throughout ontogeny the umbilicus is tiny.

The earliest whorl is inflated and the venter rounded. By a diameter of 3·5 mm the venter is sharp and the whorls are compressed, conditions which persist up to a diameter of about 35 mm. The venter is produced and sharpened to a knife-edge, a feature not fully apparent on internal moulds. Thereafter, the venter begins to broaden, being somewhat flattened at a diameter of 70–80 mm and finally in the adult rather tabulate. The juvenile flanks bear low, sinuous, fold-like ribs. Between a diameter of 20 mm and 35 mm these degenerate into discrete ventrolateral and, initially, somewhat bullate mediolateral tubercles. The maximum whorl breadth is at the level of the mediolateral tubercles, corresponding to the position of the second lateral lobe in later ontogeny, though nearer to the second lateral saddle at first. The ventrolateral tubercles become increasingly clavate during ontogeny and more prominent than the mediolaterals. At adulthood the flanks are flattened, although swollen at the mediolateral tubercles, with prominent ventrolateral tubercles bordering the tabulate venter.

The external suture shows little individual variation. The first lateral saddle is always bifid and all saddles are entire. Sutural ontogeny is shown in Fig. 14. Auxiliary saddles appear at a diameter of about 10 mm increasing in number until, at about 40 mm diameter, there is a full complement of four. Thereafter, sutural pattern is stable, although a fifth, retracted auxiliary saddle may develop. The lobes show a simple denticulate subdivision barely perceptible among the auxiliaries. Quite frequently the lobe endings are grossly truncated in immature individuals (Fig. 8). Septal fluting dies out at the centre of the septum.

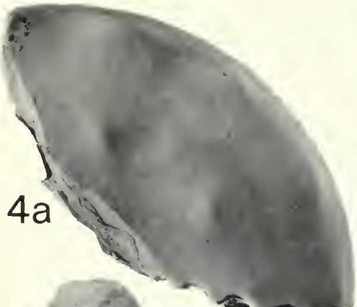
Remarks. *L. afikpoense* shows little individual, stratigraphical or geographical variation in southern Nigeria. Juvenile specimens from the Gombe region of north-eastern Nigeria (Fig. 1) described by Reyment (1955: 90; pl. 19, fig. 3; pl. 20, fig. 4) are indistinguishable from *L. afikpoense* of an equivalent size.

Libycoceras crossense sp. nov.

Figs 5, 6, 9, 11–13, 15

Name. After the Cross River, close to the locality of the type material.

Holotype. BM(NH) C.82131, about half of a mature whorl showing gross morphology, ornamentation and suture pattern (Figs 11, 15E). From the lower Nkporo Shale (Upper Campanian), about 36·5 km from Calabar on the Calabar–Ikot Ekpene road, south-eastern Nigeria.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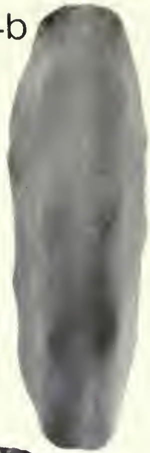
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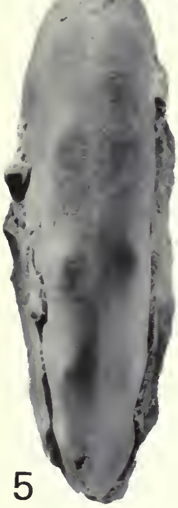
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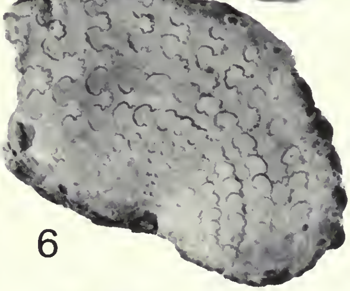
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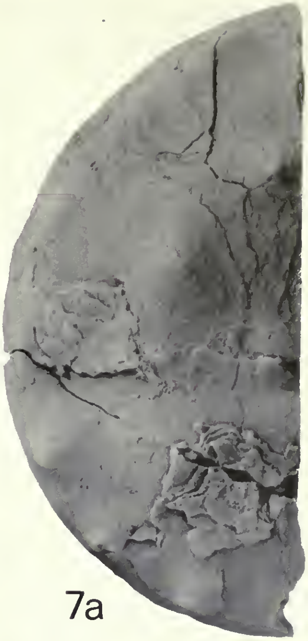
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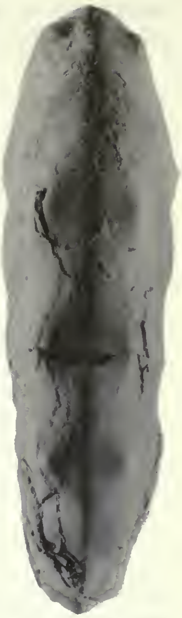
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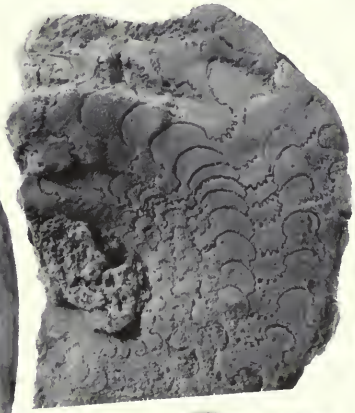
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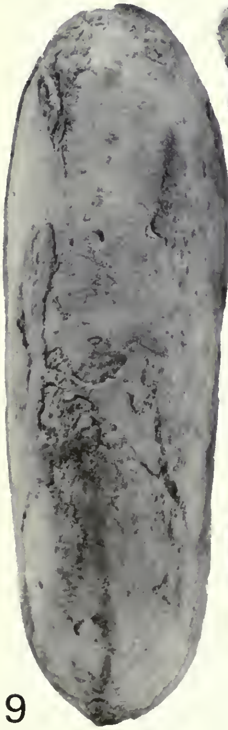
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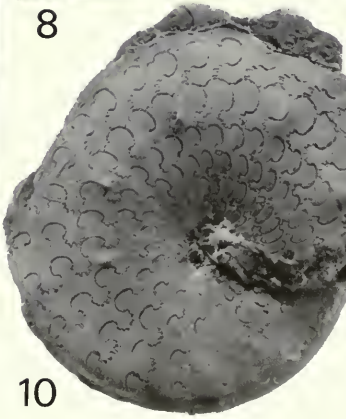
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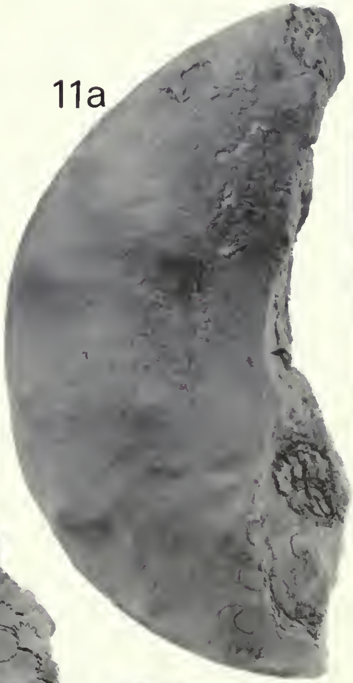
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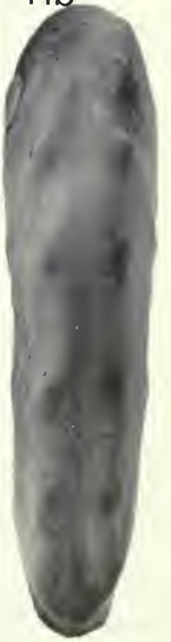
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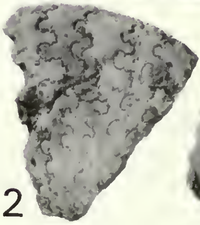
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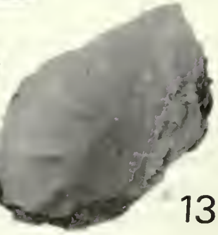
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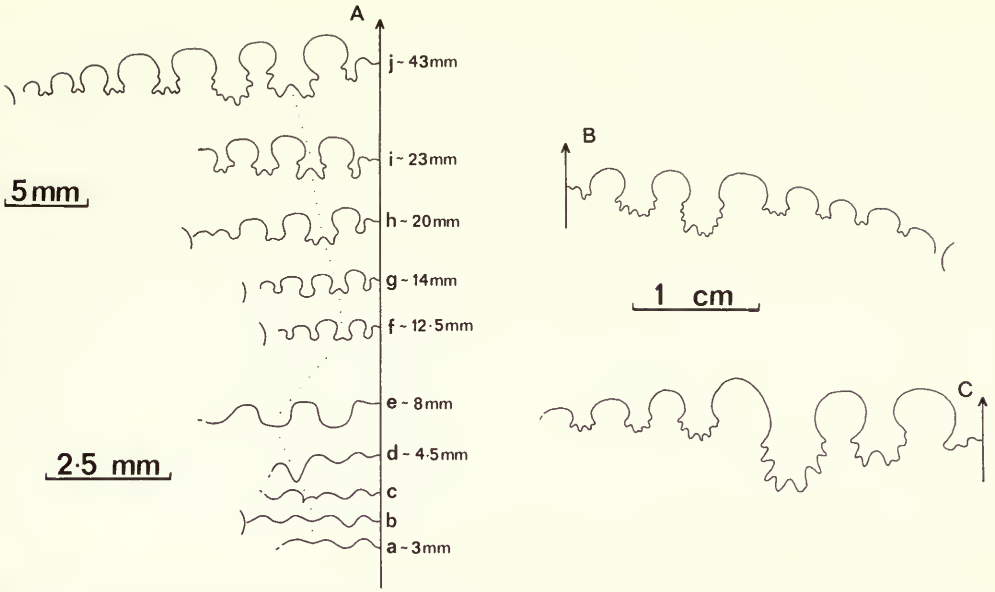

Fig. 14 External sutures in *Libycoceras afikpoense* Reyment. A, ontogenetic development of the external suture; a–d, f–j, C.83230 at diameters shown, a–d representing four successive sutures of the earliest whorl; e, UIN 423.6 at diameter shown. B, UIN 423.9 at diameter of 55 mm. C, UIN 423.19 at diameter of 80 mm. All from the basal Nkporo Shale, north-west of Calabar, south-eastern Nigeria.

Paratypes. UIN 441.1–441.34, UIN 441a.1–441a.22; C.83156–C.83169, all from the same locality as the holotype.

Other material. Twelve specimens from the Dukamaje Formation (Upper Campanian) of north-western Nigeria (C.39585, C.47245–C.47255) probably also belong in this species.

Diagnosis. *Libycoceras* with sharp venter and ornament of feeble, sinuous ribs in the juvenile. Later ornament of discrete mediolateral and ventrolateral tubercles sometimes elongated into rib-like structures. Adult venter broadly rounded with subdued ventrolateral tubercles which finally disappear. Suture with S_1 secondarily or primarily trifid. Saddles entire to weakly indented.

Description. The shell attains a diameter in excess of 130 mm, the body chamber being a little less than half a whorl in length. The umbilicus is tiny throughout ontogeny.

The earliest whorls are unknown, but at a diameter of 25 mm the shell is highly compressed with a sharp venter. The ornament here consists of low, rounded, sinuous ribs running parallel

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Figs 4, 7, 8, 10 *Libycoceras afikpoense* Reyment. Basal Nkporo Shale (Upper Campanian), about 36 km from Calabar, Calabar–Ikot Ekpene road, south-eastern Nigeria. Figs 4a, b, C.83133. Figs 7a, b, C.83135. Fig. 8, C.83137; note crowded suture lines. Fig. 10, C.83130. See also Fig. 14.

Figs 5, 6, 9, 11–13 *Libycoceras crossense* sp. nov. Lower Nkporo Shale (Upper Campanian), about 36·5 km from Calabar, Calabar–Ikot Ekpene road, south-eastern Nigeria. Fig. 5, paratype C.83159 in ventral view. Fig. 6, paratype C.83166, showing change from a bifid to trifid first lateral saddle. Fig. 9, paratype C.83160, showing nature of the adult venter. Figs 11a, b, **holotype** C.82131; see Fig. 15E. Fig. 12, paratype C.83168, showing secondary trifurcation of the first lateral saddle. Fig. 13, paratype C.83167, showing nature of the juvenile ornamentation. See also Fig. 15.

All figures natural size.

to the growth lines. The venter broadens during later ontogeny and by a diameter of about 50 mm is flattened, though slightly raised along the keel, and approaches a fastigiate condition. The ornament is now of distinct ventrolateral and less pronounced mediolateral tubercles. The tubercles may become produced into rib-like structures. The venter continues to broaden during ontogeny, though retaining a slight keel at diameters of 80–90 mm. The adult venter is smoothly rounded. Faint traces of the now clavate ventrolateral tubercles remain on the early part of the adult body chamber but disappear later. Mediolateral tubercles are not discernible on the adult body chamber.

The suture pattern is somewhat variable (Fig. 15). In most cases S_1 is bifid with the outer half bifid again, that is secondarily trifid (Fig. 15B, C). One specimen (C.83166, Fig. 6) has S_1 bifid up to a diameter of about 32 mm when a second adventitious lobe separates a small, third outer saddle. The outer saddles are entire or weakly indented. The five or six auxiliary saddles are usually entire, though the outermost may show slight indentation. Towards the top of its range north-west of Calabar, more members of this species show primarily trifid first lateral saddles (Fig. 15A, D, E). The outermost saddle so formed is smaller than the inner two. The saddles are weakly indented, their necks being fairly broad. Fluting extends over the whole septal surface, although its centre forms no more than a series of inconspicuous broad folds.

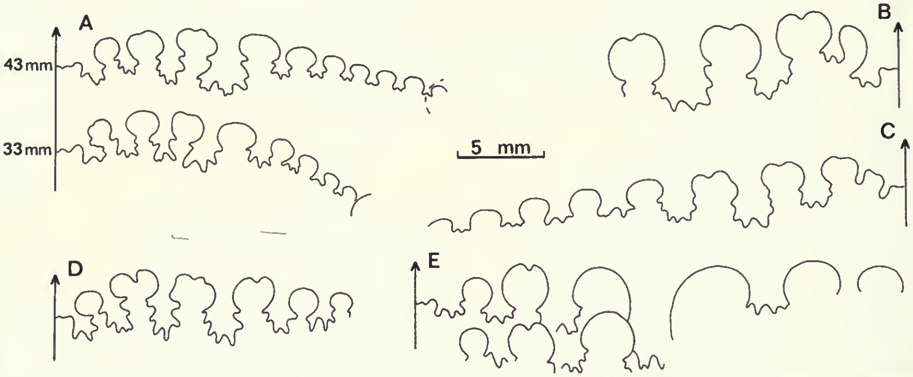


Fig. 15 External sutures in *Libycoceras crossense* sp. nov. A, paratype UIN 441.1 at diameters shown. B, paratype C.83169 at diameter of 60 mm. C, paratype C.83161 at diameter of 55 mm. D, paratype UIN 441.2 at diameter of 40 mm. E, holotype C.82131. All from the lower Nkporo Shale, north-west of Calabar, south-eastern Nigeria.

REMARKS. Although no previously-described forms referred to *Libycoceras* show a primarily trifid S_1, a number show secondary trifurcation. *L. acutodorsatum* (Noetling) and *L. pacificum* (Olsson) are examples but both develop a sharper venter and have an almost smooth shell (Noetling 1897, Olsson 1944). The *'Coahuilites'* described by Lewy (1977: 249) resembles *L. crossense* in suture pattern and its gross morphology is not very different. *'Sphenodiscus' corroyi* Sornay & Tessier and *Coahuilites (Daradiceras)* Sornay & Tessier also show a comparable suture pattern (Sornay & Tessier 1949), as do certain *Libycoceras* from the Middle East (Picard 1929: fig. 10; Lewy 1977: fig. 3), but all these differ in details of gross morphology or ornamentation.

There are specimens in the British Museum (Natural History), London, from the Dukamaje Formation at Dukamaje (C.47245–C.47255) and Gilbedi (C.39585) in north-western Nigeria (Fig. 16). These are all more or less fragmentary and weathered, but enough is visible of the suture patterns (Fig. 16) to determine that they agree closely with those in *L. crossense*. The ornament and venter breadth are also similar to *L. crossense* and they are probably conspecific.

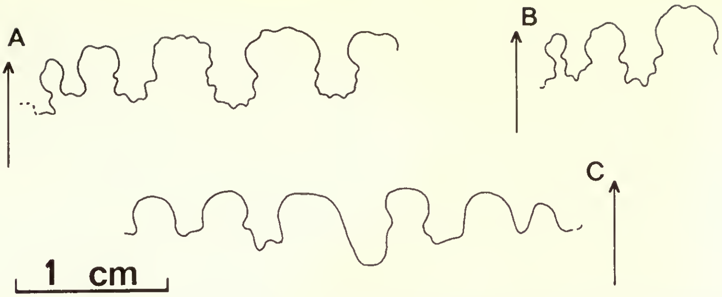


Fig. 16 External sutures in *Libycoceras* cf. *crossense* sp. nov. from the Dukamaje Formation of north-western Nigeria. A, C.47247. B, C.47251. C, C.47248. All are weathered to some degree, especially C.47248, so that full sutural details are not apparent.

Although its venter is slightly narrower and becomes rounded at adulthood, *L. crossense* is virtually indistinguishable from *L. afikpoense* on anything but suture pattern, especially in the juvenile and middle stages. The same is true of *L. crossense* and *L. ismaelis*, but in the latter the venter is frequently narrower.

Libycoceras dandense (Howarth, 1965)

Figs 17–20

1965 *Manambolites dandensis* Howarth: 396–398; pl. 12, figs 2a, 2b; pl. 13, figs 1a, 1b (with synonymy).
1970 *Manambolites* sp. gr. *dandensis* Howarth; Antunes & Sornay: 84–86; pl. I.

MATERIAL AND OCCURRENCE. The present material consists of 33 specimens (UIN 443.1–443.17; C.83211–C.83226) from the upper Nkporo Shale (uppermost Campanian to lowermost Maastrichtian) at Lokpauku, Okigwe, south-eastern Nigeria. The species is also known from strata of the same age in the Barro do Dande area of Angola from where Howarth (1965) described the holotype (C.41474) and two paratypes (C.52734, C.52736).

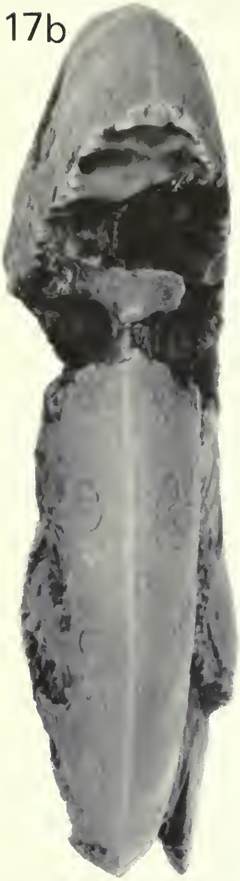
DESCRIPTION. The shell attains a diameter of some 160 mm, the body chamber being half a whorl, or a little less, in length. Throughout ontogeny the umbilicus is tiny.

Up to a diameter of 50–60 mm the whorls are highly compressed and the venter sharp. Thereafter the venter broadens, though a feeble keel is still discernible on internal moulds at diameters in excess of 100 mm. The flanks of the early whorls bear low, sinuous, fold-like ribs running parallel to the growth lines. The ribs are usually confined to the mid-parts of the flanks, and they may persist until a diameter of some 60 mm. Thereafter, the ornament consists of more or less pronounced ventrolateral tubercles, which may persist onto the adult whorl, where they may develop into low, broad ribs confined to the ventral third of the flank. In some individuals ornamentation is subdued and almost absent, especially in the early whorls. At the junction of the adult phragmocone and body chamber the venter is broadly rounded, but still has a feeble keel. The venter of the adult body chamber is not seen in the present material.

The suture (Fig. 20) always shows a trifid first lateral saddle. The outer saddle so formed is smaller than the inner two, often considerably so, and is directed obliquely to the mid-line. In early ontogeny the necks of the saddles are broad (Fig. 20A, B) but they may become constricted later on. The outer saddles are entire to fairly complexly indented. Commonly, details of their subdivision vary on opposite sides of the shell. The five or six auxiliary saddles are usually entire though the outer one may be feebly indented. Fluting extends over the whole septal surface, its centre being thrown into distinct folds and hollows.

REMARKS. The present material conforms in all important respects with the Angolan specimens described by Howarth (1965) and Antunes & Sornay (1970). The larger Nigerian collection allows a greater understanding of the variation shown within the species. Suture pattern is rather inconsistent and strength of ornamentation and sharpness of the venter also vary.

17b



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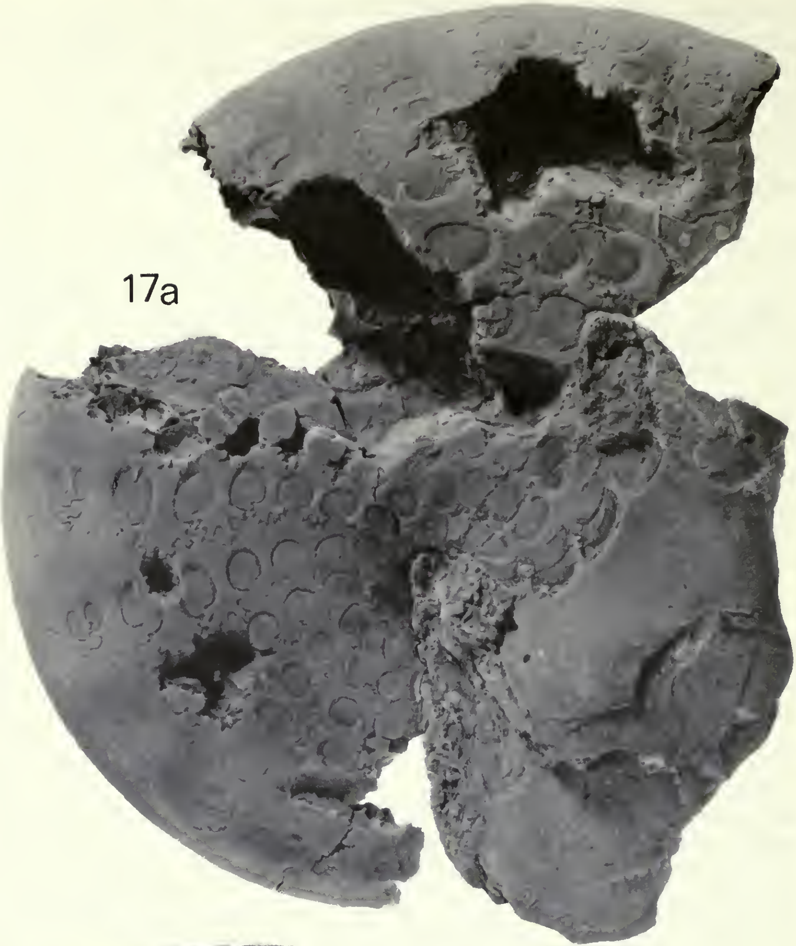

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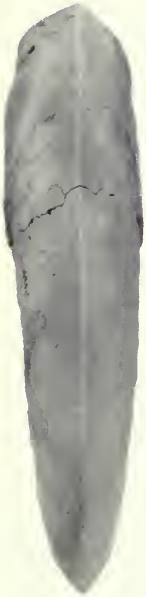

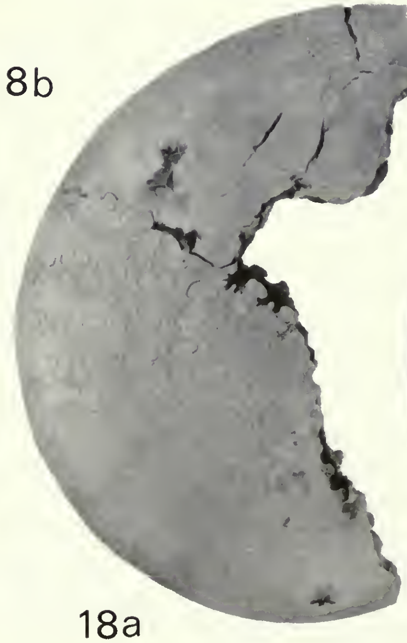

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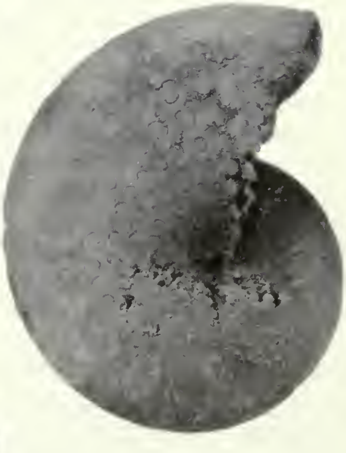
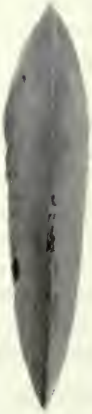


19a



19b

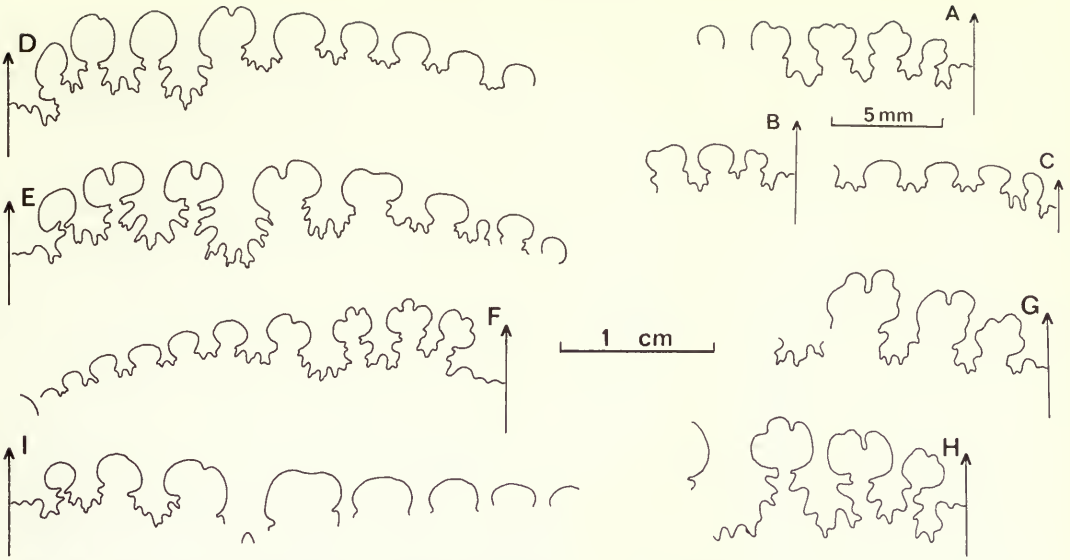


Fig. 20 Sutures in *Libycoceras dandense* (Howarth). A, UIN 443.2 at diameter of 36 mm. B, first lateral saddle in UIN 443.10 at diameter of 30 mm. C, ventral part of internal suture in UIN 443.10 at diameter of 50 mm. D, C.83226 at diameter of 70 mm. E, C.83221 at diameter of 75 mm. F, C.83216 at diameter of 55 mm. G, first lateral saddle in UIN 443.17 at diameter of 80 mm. H, first lateral saddle in UIN 443.5 at diameter of 77 mm. I, C.83219 at diameter of about 75 mm. A–C shown at greater enlargement than D–I as indicated. All from the upper Nkporo Shale, Lokpauku, south-eastern Nigeria.

In Nigeria *L. dandense* has not been found with age-diagnostic ammonites. In Angola, however, a fairly diverse associated fauna was dated by Howarth (1965: 402–405) as uppermost Campanian to lowermost Maastrichtian, an age accepted by Antunes & Sornay (1970).

The Angolan material was referred by Howarth to *Manambolites*. The stratigraphical and morphological evidence provided by the present Nigerian material, however, indicates that this species is descended from an early *Libycoceras*. Its similarities with *Manambolites* are chiefly in the nature of the adult body chamber, but differences include the generally smooth shell in that genus and its bifid first lateral saddle, which is often more highly frilled than in *L. dandense* (see Hourcq 1949). *L. crossense* also has a similar adult body chamber and its ornament is of a type similar to that in *L. dandense*, but is more strongly developed; the suture may be closely comparable though less complex in its details.

Family **SPHENODISCIDAE** Hyatt, 1900

Genus *SPHENODISCUS* Meek, 1871

Type species. *Ammonites lenticularis* Owen, 1852 (*non* Young & Bird, 1828) = *A. lobata* Tuomey, 1856; Maastrichtian, Mississippi.

The name *Ammonites lenticularis*, under which Owen (1852) first placed the type species of *Sphenodiscus*, is pre-occupied by a Liassic *Amauroceras* (Young & Bird 1828; Howarth 1958: 26). The type species is, therefore, *Ammonites lobata* Tuomey which Meek (1876) regarded as

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Figs 17–19 *Libycoceras dandense* (Howarth). Upper Nkporo Shale (uppermost Campanian to lowermost Maastrichtian), Lokpauku, Okigwe, south-eastern Nigeria. Figs 17a, b, C.83212. Figs 18a, b, C.83211. Figs 19a, b, C.83214. See also Fig. 20.
All figures natural size.

synonymous with *Sphenodiscus lenticularis* (Owen). Hyatt (1903) separated the two species, evidently on the basis of suture pattern. Since this feature is now known to be highly variable and unreliable in species designation, it appears likely that the two are actually conspecific. The holotype of *S. lobatus* is lost but Stephenson (1941: 434) has selected as neotype USNM 2403 which was figured by Hyatt (1903: pl. 7, figs 1, 2).

DISCUSSION. As mentioned above many forms previously placed in *Sphenodiscus* on the sole basis of having a trifid first lateral saddle have now been removed from the genus. Taxonomy within it is, however, still in a state of some confusion. Several authors, notably Hyatt (1903), have attempted to define species on the basis of sutural details. Whenever large numbers of specimens have been collected this character has been shown to be so variable as to be of very little use at the specific level (Stephenson 1941, Waage 1968), a fact fully supported by the discovery of the material described here. The Nigerian *Sphenodiscus* also indicate that minor ornamental details and width of the venter may be variable. Ignorance of this variation has led to proliferation of specific names for closely similar lenticular, generally smooth *Sphenodiscus* with a complex suture pattern. *S. lenticularis* (Owen), *S. lobatus* (Tuomey), *S. stantoni* Hyatt, *S. beecheri* Hyatt and *S. tirensis* Stephenson are among the more common American names. *S. siva* (Forbes, 1846) from India, *S. brasiliensis* Maury, 1930 from Brazil, and *S. ubaghsi* Grossouvre, 1894 and *S. binckhorsti* Böhm, 1898 from Europe are also similar. Related examples have been described from the Middle East (Picard 1929: 451–452), Nigeria (Reyment 1955: 87, 89) and Angola (Howarth 1965: 398–399). Stephenson (1941: 434–435), Waage (1968: 144–145) and Wolleben (1969: 326) have all pointed out the difficulties of identification at the species level. It seems clear that this genus can be divided reliably only on the basis of large population samples which show some consistent and characteristic features. It is probable that in the future many of the forms listed above will be brought into synonymy.

Sphenodiscus has always been thought of as restricted to the Maastrichtian. The American forms are of this age (see, for example, Stephenson 1923, 1941, Waage 1968, Cooper 1971). They occur widely in the Lower Maastrichtian (Gill & Cobban 1966, Gill *et al.* 1970, Cooper 1971) and in northern Mexico smooth forms range throughout 2900 m of Maastrichtian strata, extending to only 100 m below Palaeocene beds (Wolleben 1969). *Sphenodiscus* occurs in the Lower Maastrichtian of Madagascar (Collignon 1971) but in Europe it is predominantly an Upper Maastrichtian indicator (Jeletzky 1951). The association of *Sphenodiscus* with *L. ismaelis* in the Middle East (Picard 1929: 452, Lewy 1977: 245) and with *L. afikpoense* in Nigeria, however, indicates that the genus first appeared in the Upper Campanian. It is not, therefore, absolutely diagnostic of a Maastrichtian age. A *Libycoceras–Sphenodiscus* association also occurs in beds of probable Upper Campanian age in Peru (Olsson 1944).

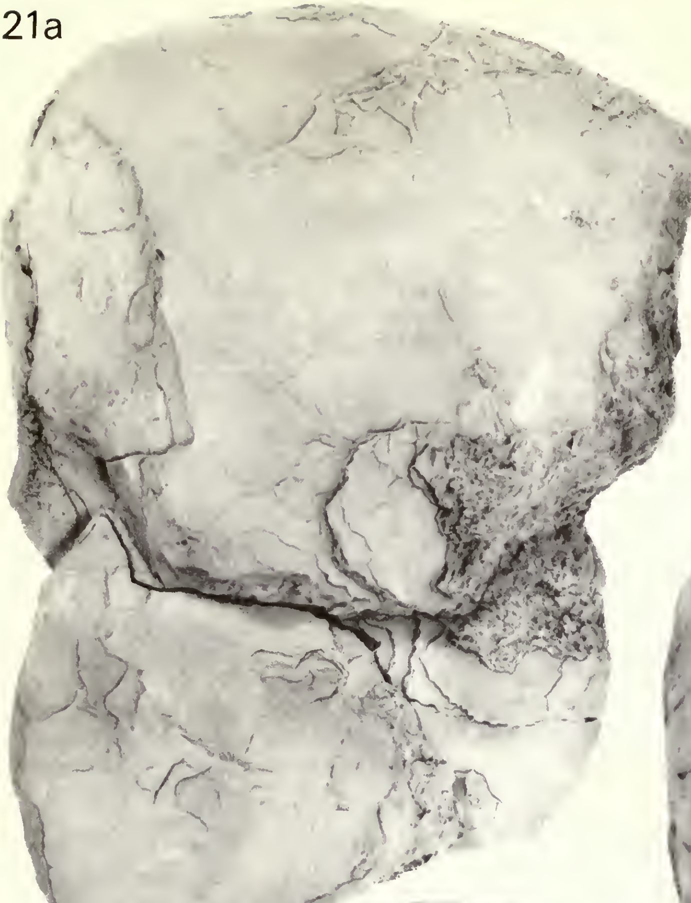
Sphenodiscus lobatus lobatus (Tuomey, 1856)
Figs 21, 24, 25

1852 *Ammonites lenticularis* Owen: 579; pl. 8, fig. 5.
1856 *Ammonites lobata* Tuomey: 168.
1871 *Ammonites (Sphenodiscus) lobatus* Tuomey; Meek: 298.
1876 *Placenticeras (Sphenodiscus) lobatus* (Tuomey) Meek: 473–476; pl. 34, figs 1a–c.
1892 *Ammonites (Sphenodiscus) lenticulare* Owen; Whitfield: 258–260; pl. 41, figs 8, 9.

Figs 21, 24 *Sphenodiscus lobatus lobatus* (Tuomey). Basal Nkporo Shale (Upper Campanian), about 36 km from Calabar, Calabar–Ikot Ekpene road, south-eastern Nigeria. Figs 21a, b, C.83128 (× 0·65). Figs 24a, b, C.83129. See also Fig. 25.

Figs 22, 23 *Sphenodiscus lobatus costatus* subsp. nov. Upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar, Calabar–Ikot Ekpene road, south-eastern Nigeria. Figs 22a, b, paratype C.83193, showing juvenile ornamentation and sharp venter. Fig. 23, paratype C.83181, showing early development of ribbing. See also Figs 26–35.

All figures natural size unless otherwise stated.

21a


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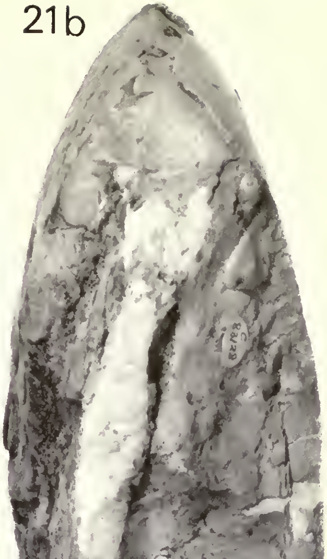

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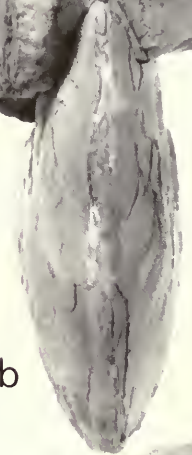

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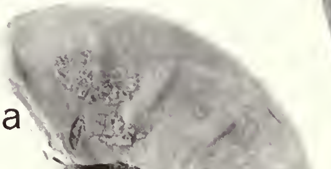

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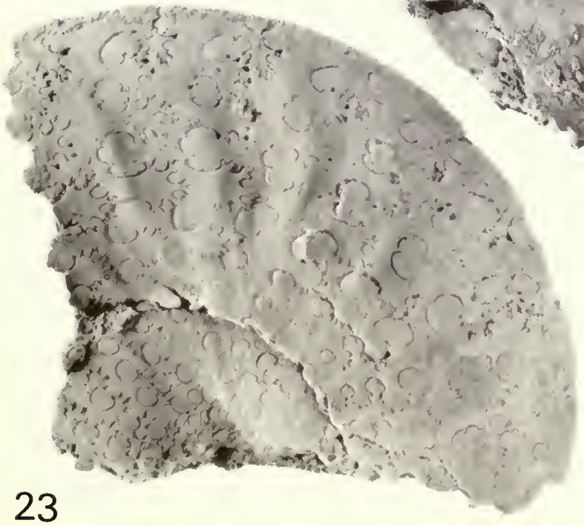

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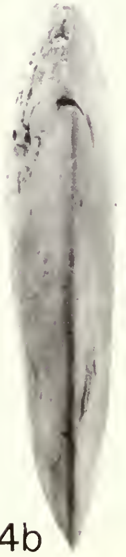

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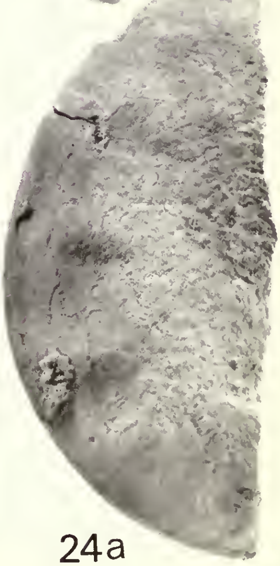


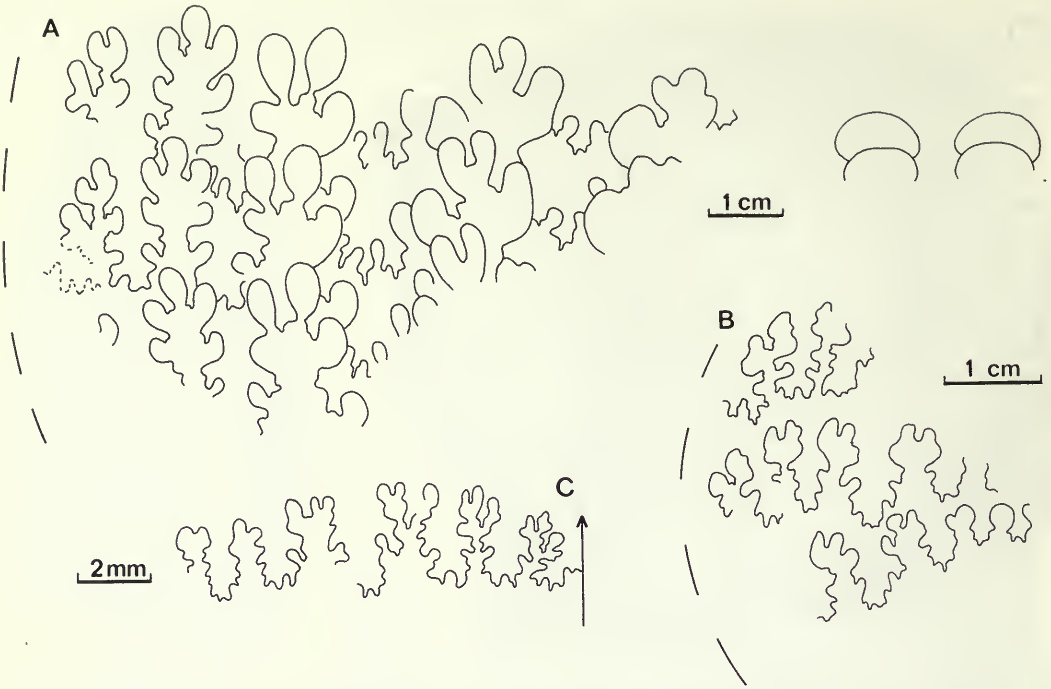


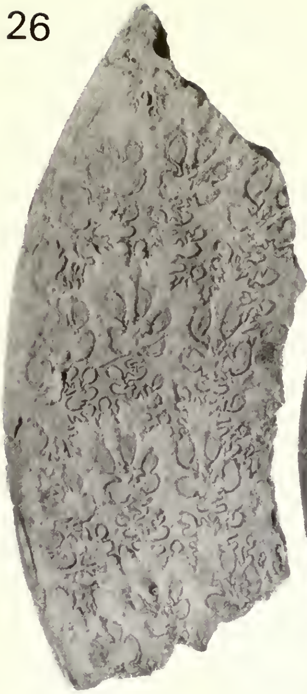
Fig. 25 Sutures in *Sphenodiscus lobatus lobatus* (Tuomey). A, C.83128 at diameter of 210 mm. B, C.83129 at diameter of about 70 mm. C, C.83229 at diameter of 20 mm. A–C shown at successively greater enlargements as indicated. All from the basal Nkporo Shale, north-west of Calabar, south-eastern Nigeria.

1903 *Sphenodiscus lobatus* (Tuomey); Hyatt: 66–70; pl. 6, figs 1, 2; pl. 7, figs 1, 2; pl. 9, figs 11–13.
1903 *Sphenodiscus lenticularis* (Owen); Hyatt: 71–75; pl. 8, figs 1, 2; pl. 9, figs 1–6.
1903 *Sphenodiscus lenticularis* var. *splendens* Hyatt: 75–77; pl. 8, figs 3–7.
1903 *Sphenodiscus lenticularis* var. *mississippiensis* Hyatt: 77–78; pl. 9, figs 7–9.
1923 *Sphenodiscus lobatus* var. *allisonensis* Stephenson: 397–398; pl. 99, figs 1, 2.
1927 *Sphenodiscus lenticularis* (Owen); Böse: 293–295; pl. 14, figs 9–11.
1929 *Sphenodiscus* sp. n., aff. *stantoni* Hyatt; Picard: 451–452.
1955 *Sphenodiscus* aff. *lobatus* (Tuomey); Reyment: 87, 89; pl. 22, figs 1a, 1b.
1955 *Sphenodiscus* sp. indet. Reyment: 89.
1962 *Sphenodiscus lobatus* (Tuomey); Reeside: 136; pl. 74, fig. 1; pl. 75, fig. 3 (with synonymy).
? 1965 *Sphenodiscus* sp. indet. Howarth: 398–399.
1965 *Sphenodiscus* aff. *lobatus* (Tuomey); Reyment: 53, 56; pl. 6, fig. 8.
1977 *Sphenodiscus* sp. n. aff. *stantoni* Hyatt; Lewy: 245.

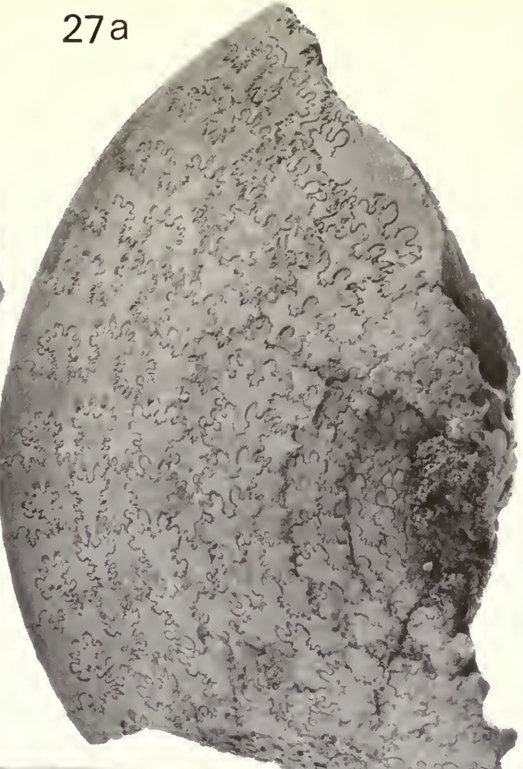
Material and occurrence. The present material consists of six specimens (UIN 445.1–445.3; C.83128, C.83129, C.83229), all from the basal Nkporo Shale (Upper Campanian), about 36 km from Calabar on the Calabar–Ikot Ekpene road, south-eastern Nigeria. The species occurs in the United States (see, for example, Hyatt 1903, Reeside 1962), the Middle East (Picard 1929)

Figs 26–28 *Sphenodiscus lobatus costatus* subsp. nov. Upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar, Calabar–Ikot Ekpene road, south-eastern Nigeria. Fig. 26, paratype C.83183. Figs 27a, b, paratype C.83173 (× 0·75). Figs 28a, b, **holotype** C.83174, showing ribbing and rounded adult venter; see Fig. 33F. See also Figs 22–23, 29–35.
All figures natural size unless otherwise stated.

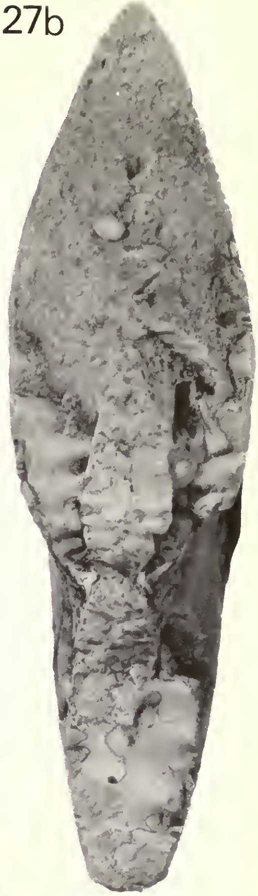
26



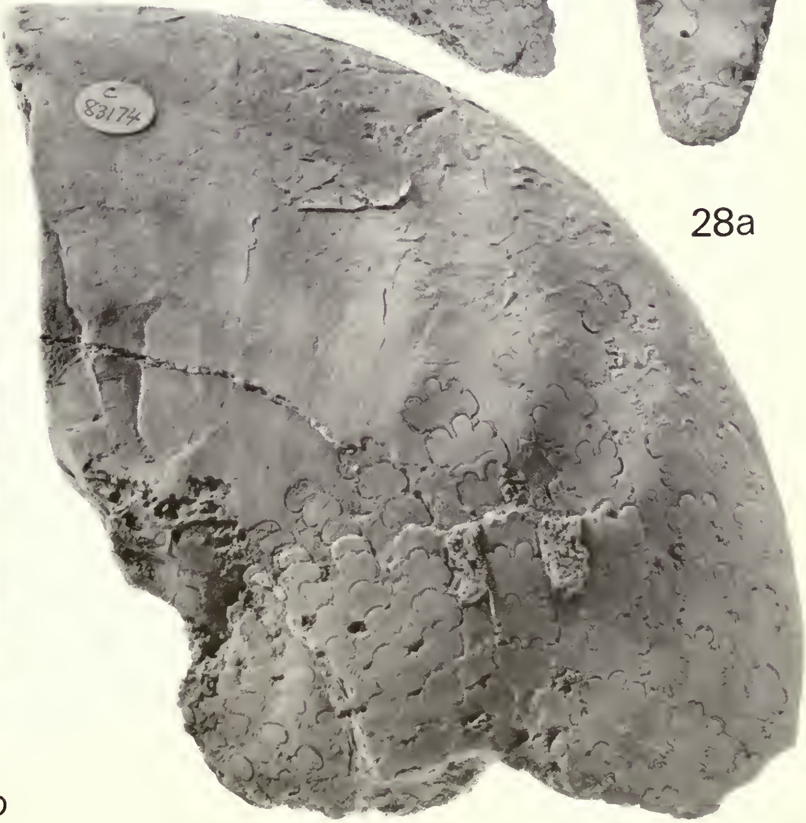
27a



27b



28a



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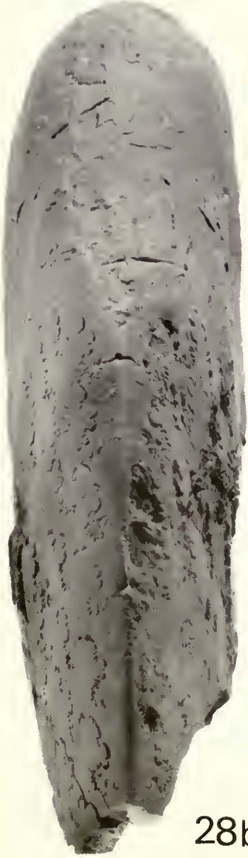


and probably also Angola (Howarth 1965). The holotype from the Maastrichtian of Mississippi described by Tuomey (1856) is believed lost, but Stephenson (1941: 434) has selected USNM 2403 as neotype.

Description. The shell attains a diameter well in excess of 200 mm. The umbilicus is nearly closed.

The earliest whorls are compressed in the available material and the venter sharpened. At diameters between 60 mm and 80 mm the flanks may bear low, bulge-like ribs tending towards a sinuous disposition which die out towards the venter and umbilicus. Other individuals are entirely smooth at this stage. Throughout the middle to early adult stages the whorls remain compressed and the venter sharp, although one somewhat distorted specimen (UIN 445.1) appears to show rounding of the venter at a diameter of only 90 to 100 mm. In the largest specimen (C.83128) the venter begins to become rounded at a diameter of some 200 mm, a trend gradually continuing until at adulthood it is narrowly but distinctly arched (Fig. 21b). The flanks here are convexly rounded and smooth apart from dense, striae-like growth lines.

The suture (Fig. 25) displays a primarily trifid first lateral saddle. The saddles are elongated and highly subdivided even in the juvenile stages. In the early whorls (Fig. 25B) there are about four auxiliary saddles which are entire or only feebly indented. In the adult there are six or more, the outer ones being divided in a fairly complex manner, the inner ones being entire. There is insufficient material available to determine the full range of sutural variation. Reyment (1955: fig. 44a) figured a further suture pattern which differs slightly from those in the present material.

Remarks. As mentioned previously it is difficult to distinguish between many of the previously-described smooth species of *Sphenodiscus*, and therefore *S. lobatus* is allowed some latitude here. Amongst the established species, *S. lobatus* is closest to the present material, and the *Sphenodiscus* described by Reyment (1955: 87, 89) is also conspecific. The individual (C.25902) from the Middle East described by Picard (1929: 451–452) differs only in the details of its sutures, and as this feature is of no great consequence in subdividing the genus, this specimen is also probably conspecific.

The distinction between this, the typical subspecies of *S. lobatus*, and *S. lobatus costatus* is discussed below.

Sphenodiscus lobatus costatus subsp. nov.

Figs 22, 23, 26–35

Name. From the concave ribs typically developed in adults.

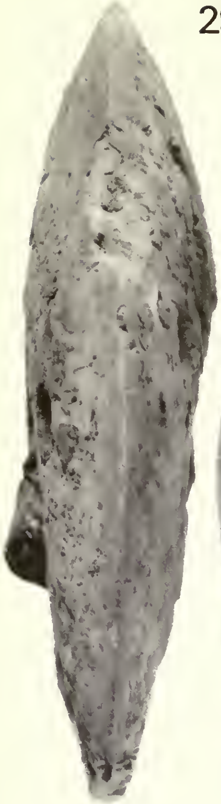
Holotype. C.83174, about one-third of an adult whorl (Figs 28, 33F) from the upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar on the Calabar–Ikot Ekpene road, south-eastern Nigeria.

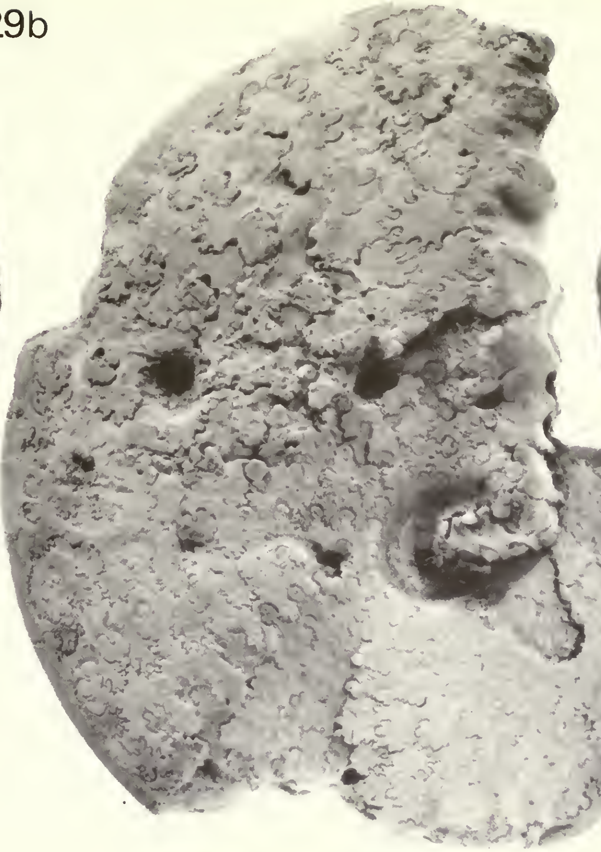
Paratypes. UIN 424.1–424.155; C.52163–C.52174, C.82133–C.82138, C.82157–C.82162, C.83172, C.83173, C.83175–C.83202, C.83228. All from the same locality as the holotype.

Diagnosis. Large *Sphenodiscus* developing a smoothly rounded venter and ornament of low, rounded, concave ribs at maturity. Middle whorls compressed with sharp venter, smooth or with ornament of more or less pronounced ribs. Sutural details highly variable.

Description. The shell attains a diameter in excess of 240 mm. The largest preserved body chambers are about half a whorl in length. The umbilicus is tiny at all stages. A slight spiral depression is often noticeable just outside the umbilical shoulder.

Figs 29–32 *Sphenodiscus lobatus costatus* subsp. nov. Upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar, Calabar–Ikot Ekpene road, south-eastern Nigeria. Figs 29a, b, paratype C.83177. Figs 30a, b, paratype C.83190, showing juvenile ornamentation and broad venter. Figs 31a, b, paratype UIN 424.1. Fig. 32, paratype C.83201. See also Figs 22–23, 26–28, 33–35.
All figures natural size.


29b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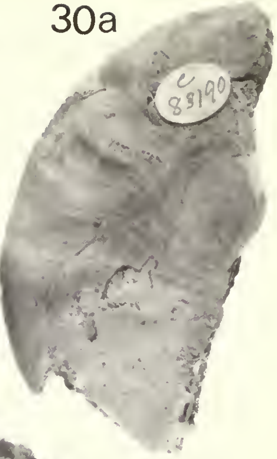

30a

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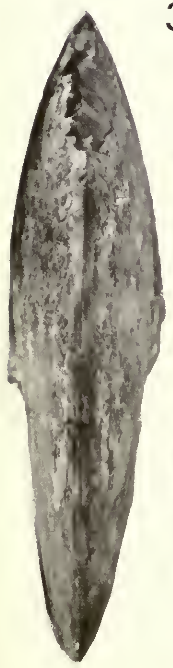
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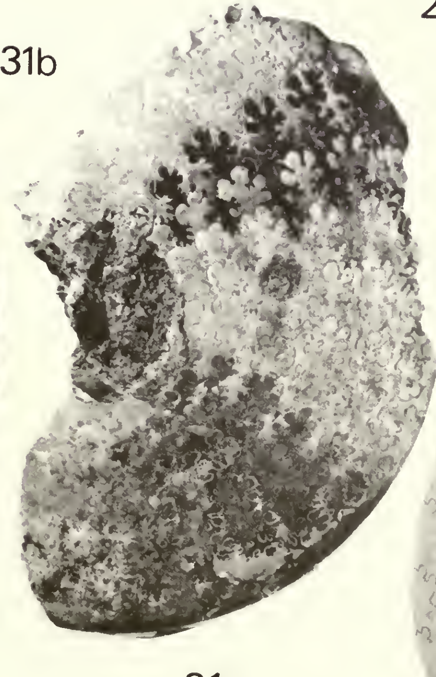
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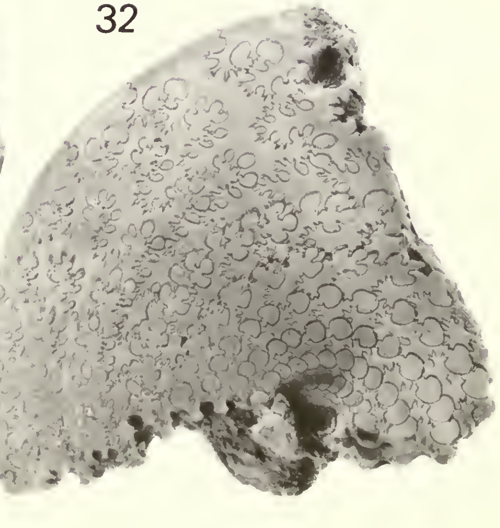

32

The early whorls are compressed, but there are several individuals preserved at diameters between about 55 mm and 70 mm which show considerable variation in the exact shape. Some have flattened flanks and a broad, almost fastigiate venter (Fig. 30b), while others are highly compressed with ventrally converging flanks and a sharp venter (Fig. 22b). The ornament at this stage is variably pronounced. Some specimens display broad, rounded, sinuous ribs which die out towards the venter and umbilicus or are expanded into broad ventrolateral bulges. Others are smooth. During middle ontogeny the whorls are almost invariably compressed, the flanks smooth and the venter sharp. In late ontogeny the venter begins to broaden and finally becomes smoothly rounded, at which stage the flanks converge ventrally only weakly. The transition may be gradual or sudden, and its timing is also variable. The venter may already be fully rounded at a diameter as low as 110 mm but in other cases there is still no appreciable rounding at diameters in excess of 165 mm. In late ontogeny an ornament of low, broad, rounded, concave ribs may appear on the ventral part of the flanks (Fig. 28a). Often distinct ribs are absent, with broad,

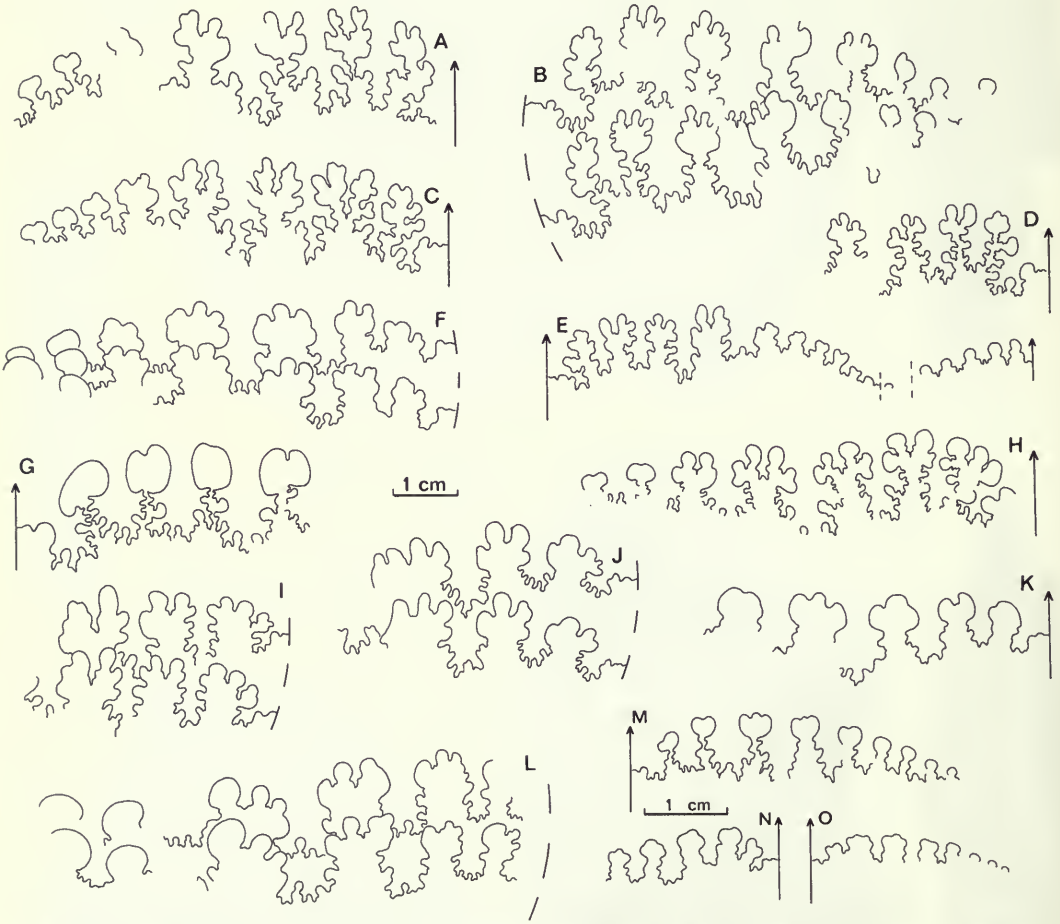


Fig. 33 Sutures in *Sphenodiscus lobatus costatus* subsp. nov. A, UIN 424.5 at diameter of 140 mm. B, C.83198 at diameter of 140 mm. C, C.83182 at diameter of 140 mm. D, UIN 424.3. E, UIN 424.7 at diameter of 95 mm, including internal suture. F, holotype C.83174 at diameter of 132 mm. G, C.52173. H, C.82157. I, UIN 424.106. J, C.83228. K, C.83175 at diameter of 180 mm. L, UIN 424.105 at diameter of 148 mm. M, UIN 424.41 at diameter of 68 mm. N, UIN 424.42 at diameter of 43 mm. O, UIN 424.147 at diameter of 42 mm. M–O shown at greater enlargement than A–L as indicated. All from the upper Nkporo Shale, north-west of Calabar, south-eastern Nigeria.

bullate tubercles developing instead. This ornamentation is generally confined to the adult body chamber, but one specimen (C.83181, Fig. 23) exhibits definite ribs at a diameter of only 100 mm. There are prominent striae-like growth lines throughout ontogeny which are clearly visible even on internal moulds.

The suture pattern is highly variable throughout ontogeny (Fig. 33). The first lateral saddle is invariably trifid, with the outermost division commonly showing a tendency towards another bifid division. The first and second lateral saddles may be elongated, narrow-necked and phylloid at one extreme, or squat, broad-necked and simply subdivided at the other. The saddle endings are occasionally entire (Fig. 33G). There is no consistency in the details of the saddle endings and they may be asymmetrically developed on opposite sides of the shell. The six or seven auxiliary saddles may be divided, often in a complex manner, or simply indented to entire especially in forms with broad-necked saddles. It is possible to trace a partial correlation between size and suture pattern. Immature forms usually show phylloid saddle endings, while adults tend to display squatter elements. This ontogenetic trend is shown in some fairly complete specimens but is again inconsistent. The juvenile sutures are also highly variable (Fig. 33 M–O). Fluting extends over the whole septal surface, its centre being thrown into conspicuous folds and hollows.

REMARKS. The large amount of material available admirably displays the great variation to be expected in this form. The most highly variable features are the juvenile ornamentation and whorl shape, timing of rounding of the venter, adult ornamentation and particularly the sutural details. These features are therefore of little use in taxonomic subdivision. The most diagnostic feature of this subspecies is the ribbed adult ornament, but since this feature is often poorly developed a large amount of material is necessary for accurate diagnosis. The juvenile and middle whorls on the other hand are, for all practical purposes, indistinguishable from those in *S. lobatus lobatus*, and since the sutures also correspond, the two forms are separated only at the subspecies level. Stephenson (1941: 435) mentions 'faint, widely spaced, broad, low radial swells' in the adult of *S. tirensis* but these do not appear to be as pronounced as the ornament in the present material and they are not evident on his plates.

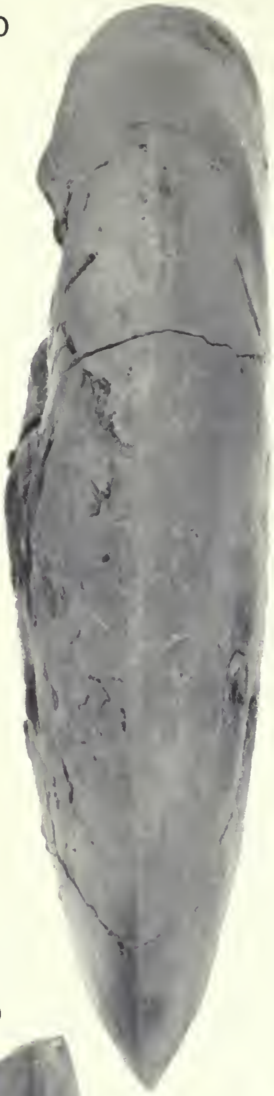
As previously mentioned, *Sphenodiscus* ranges from Upper Campanian to Upper Maastrichtian in age. The association of *S. lobatus costatus* with *Pachydiscus (P.)* aff. *dossantosi* and *P. (Neodesmoceras)* sp. makes a Lower Maastrichtian age most likely for the present material. *P. (P.) dossantosi* occurs in the Maastrichtian of Brazil (Maury 1930) and a very similar form occurs in the Maastrichtian of Peru in beds overlying levels containing a *Libycoceras–Sphenodiscus* association (Olsson 1944). *Neodesmoceras* is primarily a Maastrichtian form. It occurs in the Lower Maastrichtian of Madagascar (Collignon 1955, 1971) and throughout the Maastrichtian of Japan (Matsumoto 1977). In Alaska and South Africa, however, it may range down into the Upper Campanian (Jones 1963, Kennedy & Klinger 1975).

The author is grateful to Dr A. Dhondt and Dr N. J. Morris for identification of some inoceramids occurring in association with *S. lobatus costatus* in the Calabar section. These bivalves indicate an age not younger than Lower Maastrichtian.

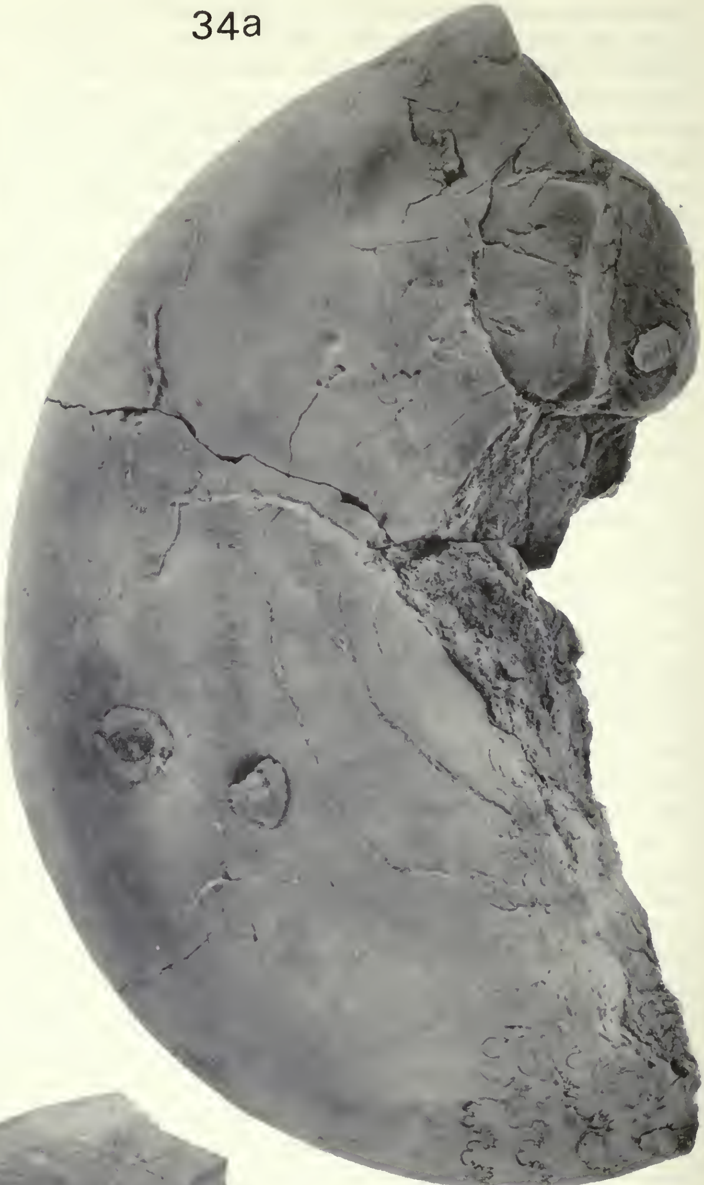
Interrelationships within the family Sphenodiscidae

A major problem in sphenodiscid phylogeny has been the lack of observed faunal successions. In Texas and northern Mexico species of *Coahuilites* and *Sphenodiscus* are common and inferred successions were used by Böse & Cavins (1927) to establish a zonation for the region. The basis for these zones was called into question by Waage (1968) and Wolleben (1969). Cooper (1971), however, rationalized the taxonomy of these stocks and presented a modified zonal scheme. Unfortunately, there is limited information provided on the phylogeny of the family by these forms. Phylogeny has, therefore, largely been inferred on morphological grounds. Picard (1929: 453) implied a progressive increase in complexity of suture pattern during phylogeny while Reyment (1956: 75–76) proposed an opposite view, deriving

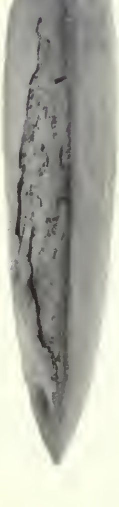
34b

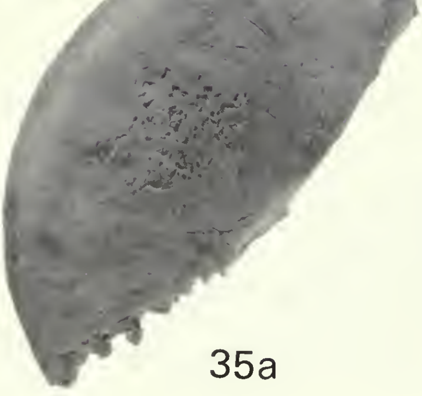


34a



35b





35a

Libycoceras from *Sphenodiscus*. The present Nigerian material clarifies these issues considerably.

In the Calabar region of Nigeria *L. crossense* appears immediately above *L. afikpoense* in the Nkporo Shale. *L. dandense* occurs at Lokpauku in the Nkporo Shale just below the diachronous Mamu Formation. It belongs to a level corresponding to the unexposed middle part of the Nkporo Shale north-west of Calabar (Fig. 3, p. 307). This conclusion is supported by the relative dating of these species. A *L. afikpoense–L. crossense–L. dandense* succession exists, therefore, these species representing a definite lineage displaying progressive morphological change which can be summarized as follows:

1. An increase in sutural complexity. The major trend here involves secondary trifurcation followed by primary trifurcation of S_1. In addition the outer saddles become more complexly indented with narrower necks; the auxiliary saddles increase in number, the outer ones becoming indented, and fluting extends to cover the whole of the septal surface.
2. A reduction in ornamentation. Although juvenile ornamentation is similar in all three species it becomes markedly reduced in adults. The mediolateral tubercles are reduced the more rapidly, the ventrolaterals persisting in an obsolete condition in *L. dandense.*
3. An increase in whorl compression. The juvenile whorls are again similar in all three species as regards their gross morphology. Later species display a lesser broadening of the venter during growth although even in *L. dandense* it is fairly broadly rounded in the adult.

It is worth mentioning also that individual variation increases markedly in later species.

L. dandense may well be derived directly from *L. crossense.* The latter species may be derived either from *L. afikpoense* or from North African stocks of *L. ismaelis.* The probable presence of *L. crossense* in north-western Nigeria and its abrupt appearance in the Calabar section supports the last suggestion.

It is evident that *L. dandense* has a morphology close to that of *Sphenodiscus*, and on purely morphological grounds it could be accommodated in that genus. If later members of its lineage existed, they might be expected to be almost indistinguishable from *Sphenodiscus*. It is of interest, therefore, to consider *S. studeri* (Reyment 1955, 1957). This species was dated by Reyment (1956, 1965) as lower Upper Maastrichtian, evidently because of its stratigraphical position closely below definite Palaeocene beds. In the absence of more direct evidence, however, the possibility remains that it is somewhat older. The species is represented by a single, imperfect internal mould (C.48050). Its morphology recalls that in *L. dandense*. There are traces of a feeble ornament of ribs in the early whorls and of ventrolateral and weak mediolateral tubercles in the later stages. Rounding of the venter occurs at an early diameter of about 85 mm. The suture pattern is moderately complex. Conceivably *S. studeri* is derived from *Libycoceras.*

The southern Nigerian *Libycoceras* species were short-lived. They would, therefore, seem to offer a satisfactory basis for detailed correlation in the Upper Campanian and Lower Maastrichtian strata of the region.

Those smooth or ornamented *Libycoceras* showing tendencies towards trifurcation of S_1, such as *L. acutodorsatum* (Noetling 1897), *L. spathi* (Picard 1929), *'Daradiceras'* and *L. corroyi* (Sornay & Tessier 1949) and the *'Coahuilites'* described by Lewy (1977), most probably represent variants of a stock derived, like *L. crossense*, from earlier *Libycoceras* showing a simple, bifid first lateral saddle.

Indoceras has a suture pattern very close to that shown in the early *Libycoceras* species, with a bifid S_1 and all saddles entire (Noetling 1897). It is distinguished chiefly by its smooth shell and by its rounded venter during the middle and adult growth stages, in which respects it resembles *Manambolites* (Hourcq 1949). Similar features to these, however, are known in certain

Figs 34, 35 *Sphenodiscus lobatus costatus* subsp. nov. Upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar, Calabar–Ikot Ekpene road, south-eastern Nigeria. Figs 34a, b, paratype C.82171, an adult showing development of a rounded venter and traces of ribbing (×0·65). Figs 35a, b, paratype C.83189, a juvenile lacking ornament and showing a sharp venter (×1). See also Figs 22–23, 26–33.

Libycoceras, and *Manambolites* has frilled outer saddles in the suture. It would appear, therefore, that *Indoceras* has its closest affinities with *Libycoceras*, though the only known species seems to appear later than *Libycoceras*, being probably of Lower Maastrichtian age (Reiss 1962: 9).

Specimens from eastern Mali referred by Ilyin *et al.* (1970) to *Indoceras africanense* Ilyin do not show the distinctive rounding of the venter characterizing that genus. These large, feebly ornamented, highly compressed forms appear identical to material from the same area described by Pérébaskine (1930), which he considered to represent a new variety of *Libycoceras ismaelis*, *L. ismaelis* var. *soudanense*. Pérébaskine's material was collected along with broader, more typical *L. ismaelis* from a horizon said to be close to the base of the calcareous beds of the region (Pérébaskine 1930: 131). These calcareous beds ('Terme IV' of Greigert 1966) were formed during a transgressive episode affecting eastern Mali and extending as far south as the Mali–Niger border (Greigert 1966, Greigert & Pougnet 1967). Greigert (1966: 81–83, 85; pl. 44) dated them as latest Maastrichtian to early Palaeocene. Ilyin *et al.* (1970), however, assigned a Danian age since they contain the foraminifer *Laffitteina bibensis* Marie, a Danian index for this region (see also Berggren 1974). South of Mentess on the Mali–Niger border these beds occur above the '*Mosasaurus* Shales' (= Dukamaje Formation in north-western Nigeria), being separated from them by a sandy regressive sequence (Greigert 1966: pl. 44, Ilyin *et al.* 1970: fig. 1). The '*Mosasaurus* Shales' represent an earlier transgression affecting western Niger and north-western Nigeria. In Niger they contain *Libycoceras ismaelis* (Greigert & Pougnet 1967: 139), and in their extension into north-western Nigeria they also yield *L.* cf. *crossense*. It is most likely that *Indoceras africanense* is in fact a variety of *L. ismaelis*, synonymous with *L. ismaelis* var. *soudanense* of Pérébaskine (1930). It seems, therefore, that, in eastern Mali at least, this species persisted until the end of the Maastrichtian. By Maastrichtian times in southern Nigeria, however, *L. dandense* had already appeared.

Sphenodiscus is also a long-lived and apparently conservative genus. Smooth forms were thought by Wolleben (1969) to represent a root stock giving off successive 'tribes' at various intervals. There is some evidence to suggest that the distinctly ornamented species (*S. pleurisepta* (Conrad) and its allies) appear later than the smooth *Sphenodisus* (Böse 1927, Cooper 1971). *S. lobatus costatus* certainly appears to have been derived from a smooth *S. lobatus lobatus*-like form. The precise relationship between the smooth and ornamented forms is, however, unclear (see also Waage 1968: 144) and there may be no clear-cut distinction between the two groups. If this genus is to be of widespread use in correlation, it is clear that Stephenson (1941) and Wolleben (1969) are correct in stating that a full understanding of its evolution based on large population samples will be necessary. A further complication here is that this genus may sometimes show a preference for abnormal marine environments (Waage 1968: 144).

Since *Sphenodiscus* appears as early as *Libycoceras* in the Upper Campanian it is unlikely to have been derived from that genus by complication of suture pattern. Rather it may be descended from early Campanian members of the Lenticeratinae, or from *Placenticeras* which occurs below the *Sphenodiscus*-bearing beds in Texas and northern Mexico (Böse 1927, Cooper 1971). It is, nevertheless, true that certain *Libycoceras* species come to resemble *Sphenodiscus* morphologically.

The earliest known sphenodiscid is *Manambolites piveteaui* Hourcq (1949), which appears at the base of the Middle Campanian in Madagascar (Besairie & Collignon 1960: 79). This genus is probably derived from *Eulophoceras* from which it differs mainly in its rather simpler suture (see Hourcq 1949: figs 4, 5, 20, 21). For *Libycoceras* to be derived from *Manambolites*, however, would be less plausible, since this would require further simplification of suture pattern followed immediately by a rapid increase in complexity and an equally rapid development and subsequent loss of ornamentation. The ancestors of *Libycoceras*, therefore, remain obscure and it may be necessary to seek them among earlier pseudoceratites.

'Manambolites' ricensis Young (1963: 127–128) is a peculiar form of uncertain generic status. *Coahuilites (Mzezzemceras) pervinquieri* Basse (1954) is either related to *Manambolites* (Howarth 1965: 395) or to those *Libycoceras* species which show sutural complication.

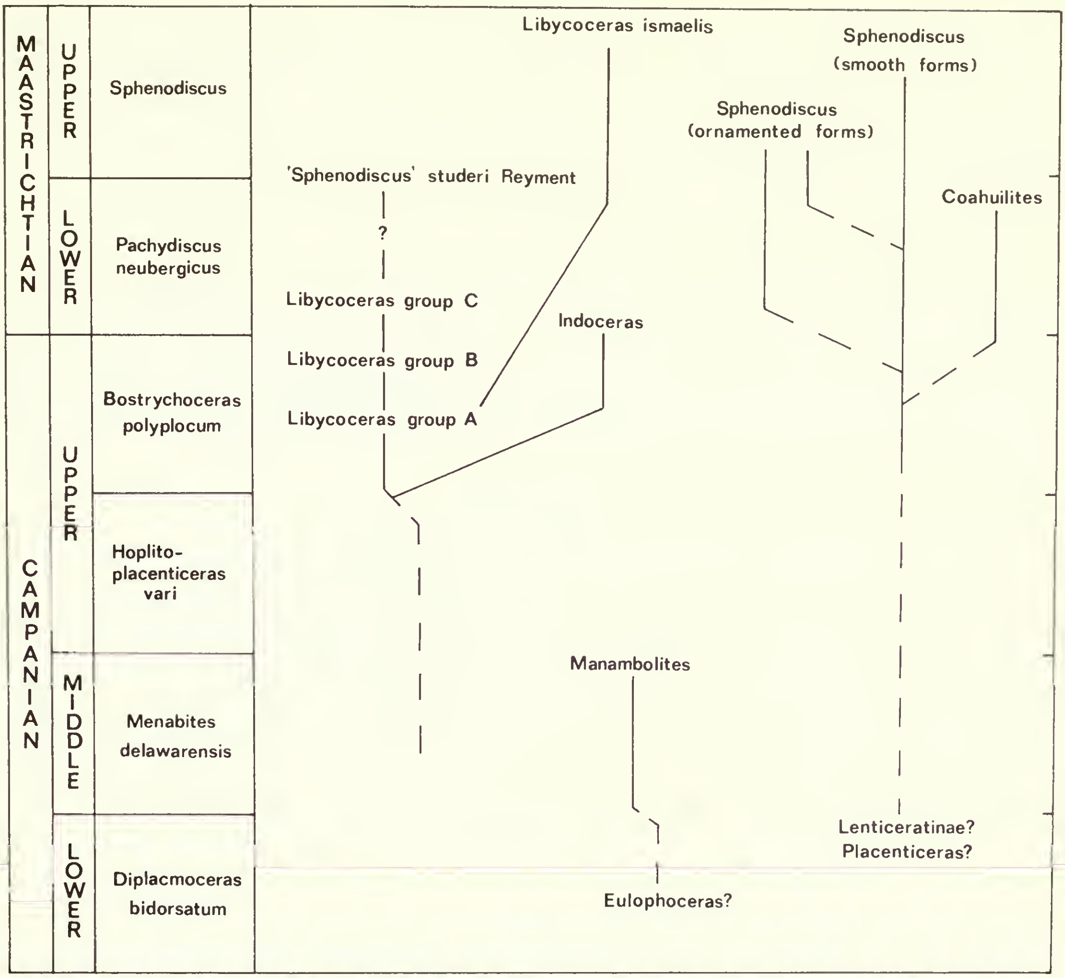

MAASTRICHTIAN
UPPER
Sphenodiscus
LOWER
Pachydiscus neubergicus
CAMPANIAN
UPPER
Bostrychoceras polyplocum
Hoplito-placenticeras vari
MIDDLE
Menabites delawarensis
LOWER
Diplacmoceras bidorsatum
Libycoceras ismaelis
Sphenodiscus (smooth forms)
Sphenodiscus (ornamented forms)
'Sphenodiscus' studeri Reyment
?
Coahuilites
Libycoceras group C
Indoceras
Libycoceras group B
Libycoceras group A
Manambolites
Lenticeratinae?
Placenticeras?
Eulophoceras?

Fig. 36 Diagram showing the inferred phylogenetic relationships within the families Sphenodiscidae and Libycoceratidae. *Libycoceras* group A includes *L. ismaelis* (Zittel), *L. afikpoense* Reyment, *L. angolense* Haughton and *L. chargense* Blanckenhorn. *Libycoceras* group B includes *L. crossense* sp. nov. and probably *'Paciceras'* Olsson, *'Sphenodiscus' acutodorsatum* Noetling, *'S.' spathi* Picard, *'S.' corroyi* Sornay & Tessier, *'Daradiceras'* Sornay & Tessier and *'Coahuilites'* (Lewy 1977). *Libycoceras* group C includes *L. dandense* (Howarth).
Note that in eastern Mali at least *L. ismaelis* persists until the end of the Maastrichtian.

The only other sphenodiscid genus generally recognized is *Coahuilites*. Cooper (1971) brought the three species described by Böse (1927) into synonymy. The genus occurs intimately mixed with *Sphenodiscus* in Texas and northern Mexico and Waage (1968: 144) expressed doubt about the separation of the two genera. The major distinction between them lies in the bifid nature of the first lateral saddle in *Coahuilites*. Certain *Sphenodiscus* show secondary trifurcation of S_1 (Olsson 1944: 108–110, Howarth 1965: 395, fig. 22), and a similar condition exists in *Coahuilites* (Böse 1927: 288, 291; pl. 14, figs 1, 3, 7, 8). In this, and also in ornament, there is thus overlap between *Coahuilites* and certain *Sphenodiscus* (Böse 1927: pl. 16, Hyatt 1903: pl. 6, fig. 6). Böse (1927: 282) considered *Coahuilites* to appear earlier than *Sphenodiscus* but this was disputed by Cooper (1971). Probably *Coahuilites* is a derivative of *Sphenodiscus* perhaps warranting separation only at subgeneric level.

It appears likely, therefore, that the family Sphenodiscidae as currently defined is not a monophyletic group. The possible interrelationships between these forms are shown in Fig. 36. The major conclusion to be drawn from the present study is that *Libycoceras* and *Indoceras* on the one hand and *Sphenodiscus* and *Coahuilites* on the other belong to separate stocks. It is necessary to separate them taxonomically, and the family Libycoceratidae is here proposed to accommodate the first two genera. The precise relationship of *Manambolites* to the abovementioned genera remains unclear.

Acknowledgements

Warm thanks are due to Dr M. K. Howarth for help in many ways, including criticism of the manuscript. Mr D. Phillips also provided much assistance. The Cross River State Government kindly gave permission for necessary field work. Mr T. Ijadunade assisted in the collecting. Photographs were provided by the British Museum (Natural History) Photographic Unit. This work was completed while the author was in receipt of a University of Ilorin Senate Research Grant.

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Accepted for publication 19 May 1982

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